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Alabagrus Enderlein (Hymenoptera, Braconidae, Agathidinae) Species of Costa Rica, with an Emphasis on Specimens Reared from Caterpillars in Área de Conservación Guanacaste[1]

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ABSTRACT. Eighty-six species of Costa Rican *Alabagrus* are treated; these include species reared from lepidopteran larvae in Área de Conservación Guanacaste, Costa Rica, over 32 years of caterpillar inventory. Sixty-five new species are described, that is, *A. almasolisae*, *A. andresfreitasi*, *A. andywarreni*, *A. axelhausmanni*, *A. barbsharanowskiae*, *A. bernardoespinozai*, *A. bobpoolei*, *A. bobrobbinsi*, *A. bobwhartoni*, *A. brendameierottoae*, *A. brianbrowni*, *A. brianharrisi*, *A. craigevansi*, *A. donharveyi*, *A. donlafontainei*, *A. fernandezi*, *A. fernandodiasi*, *A. genemonroei*, *A. hansoni*, *A. hespenheidei*, *A. iankitchingi*, *A. ilgookangi*, *A. isidrochaconi*, *A. jackiemillerae*, *A. jeanfrancoislandryi*, *A. jeanmariecadioui*, *A. jennyphillipsae*, *A. jimmilleri*, *A. johnbrowni*, *A. johnburnsi*, *A. johnobryckii*, *A. johnsharkeyi*, *A. kaciejoae*, *A. karensharkeyae*, *A. kaydodgeae*, *A. keithwillmotti*, *A. leedyeri*, *A. lindapitkinae*, *A. longinoi*, *A. malcolmscoblei*, *A. marcepsteini*, *A. mariaheikkilae*, *A. markmetzi*, *A. mattottoi*, *A. nickgrishini*, *A. patsharkeyi*, *A. paulgoldsteini*, *A. paulheberti*, *A. paulsharkeyi*, *A. paulthiaucourti*, *A. quickei*, *A. ramyamanjunathae*, *A. reddypallii*, *A. rudolfmeieri*, *A. sarahmeierottoae*, *A. sarahsharkeyae*, *A. scottmilleri*, *A. scottshawi*, *A. semihespenheidei*, *A. stiremani*, *A. tanyadapkeyae*, *A. tommyersi*, *A. victoriapookae*, *A. yuanmaofangi*, and *A. yuchinkengae*.

Species limits primarily based on cytochrome *c* oxidase subunit I mitochondrial DNA sequence data greatly differed from previous morphological attempts to delimit species of *Alabagrus*. As a result, 17 species reported to occur in Costa Rica are no longer considered to be present in the country, that is, *A. albispina*, *A. imitatus, A. juchuy*, *A. kagaba*, *A. latisoma*, *A. latreillei*, *A. maya*, *A. mojos*, *A. nahuatl*, *A. nigrilitus*, *A. pachamama*, *A. paruyana*, *A. parvifaciatus*, *A. semialbus*, *A. tricarainatus*, *A. tripartitus*, and *A. warrau*. Furthermore, five species have been found to be composed of species complexes, that is, *A. cocto*, *A. englishi*, *A. pecki*, *A. roibasi*, and *A. yaruro*. These difficulties point to the impossible task of delimiting species of Agathidinae solely with morphological evidence.

An illustrated key to species, and a plate of color photos of each species are provided.

INTRODUCTION

This article is the third in a series revising the species of Agathidinae reared from lepidopteran caterpillars as part of the inventory of the caterpillars and their parasitoids of Área de Conservación Guanacaste (ACG), northwestern Costa Rica (http://janzen.sas.upenn.edu; http://www.acguanacaste.ac.cr; Janzen et al., 2009). It includes a key to 87 species of *Alabagrus* Enderlein, of which 65 are newly described. This is not meant to be a comprehensive treatment of the Costa Rican fauna of *Alabagrus*. A conservative estimate, based on extensive collections at Instituto Nacional de Biodiversidad (INBio; Costa Rica), the Universidad de Costa Rica, and the Hymenoptera Institute (Lexington, Kentucky), is that about 300 species occur in the country.

New World members of *Alabagrus* may be distinguished from other agathidines by the following combination of character states: simple claws with a basal lobe, frons bordered laterally by carinae; first metasomal median tergite distinctly convex and/or with a median ridge, gena not elongate. All are presumed to be koinobiont endoparasitoids of concealed larvae of Crambidae. *Pharpa* Sharkey, 1988, is the sister group to *Alabagrus* (Sharkey, 1988) and is used here as the outgroup for the phylogenetic analyses. Both genera are restricted to the New World.

We include a molecular data set consisting of 680 *Alabagrus* operational taxonomic units (OTUs) sequenced for cytochrome *c* oxidase subunit I (*COI*) for approximately 60 species. The majority of specimens (624) were reared from caterpillars (those with specimen numbers beginning with DHJPAR).

Alabagrus was first revised by Sharkey (1988), who included 104 species. Leathers and Sharkey (2003) revised the species of *Alabagrus* of La Selva, and included previously described species known to occur in Costa Rica. They treated 39 putative species, including six new species. These two revisions relied solely on morphological evidence. The species concepts in the present treatment were formulated with the assistance of *COI* sequence data and a plethora of host data as the result of rearings in Área de Conservación de Guanacaste. These data have had a profound effect. There are many more cryptic species than previously thought, and many species with presumed wide distributions are more likely to be species complexes whose component species have relatively restricted distributions. As a result, 17 species, reported to occur in Costa Rica by Leathers and Sharkey (2003), are no longer considered to be present in the country, these are *Alabagrus albispina*, *A. imitatus*, *A. juchuy*, *A. kagaba*, *A. latisoma*, *A. latreillei*, *A. maya*, *A. mojos*, *A. nahuatl*, *A. nigrilitus*, *A. pachamama*, *A. paruyana*, *A. parvifaciatus*, *A. semialbus*, *A. tricarainatus*, *A. tripartitus*, and *A. warrau*. Furthermore, five of the species reported by Leathers and Sharkey (2003) have been found to be composed of species complexes, that is, *Alabagrus cocto*, *A. englishi*, *A. pecki*, *A. roibasi*, and *A. yaruro*. These difficulties point to the impossible task of delimiting species of Agathidinae solely with morphological evidence.

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[1] URL: www.nhm.org/scholarlypublications

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METHODS

SPECIMEN INFORMATION

Most specimens used in this study are deposited in the Entomology Museum of Utah State University and the Hymenoptera Institute Collection, with the exception of specimens with numbers beginning with "BIOUG," which are deposited at the University of Guelph, Centre for Biodiversity Genomics, Ontario, Canada. Source files for the keys, descriptions, illustrations, DNA sequences and distributional data are all freely available to future researchers who may wish to build on these records. The detailed specimen records are available by search of the individual specimen DHJPARxxxxxxx voucher codes at the Janzen database (http://janzen.bio.upenn.edu/caterpillars/database.lasso). Some of the Lepidoptera hosts are incompletely identified; however, they also have unique names, such as *Desmia* Solis19 (which is an interim name for *Desmia* species 19 as determined by M. Alma Solis of the U.S. Department of Agriculture Systematic Entomology Laboratory, Washington, D.C.). These names will be updated in the Janzen database when the species is baptized with a formal scientific name, but the interim name, in this case *Desmia* Solis19, will remain searchable in that database. Host caterpillars are uniquely identified by their own voucher code system, which is recognizable by YY-SRNP-XXXXX, where YY is the two-digit year and XXXXX is a unique number within that year.

DNA trace files and primer information are available through the Barcode of Life Data Systems (BOLD, http://www.boldsystems.org; Ratnasingham and Hebert, 2007), as is specimen information for specimen numbers INBxxxxxxxxxx, INBIOCRIxxxxxxxxx, and BIOUGxxxxx-xxx. Specimen information for specimens with numbers beginning with the letter "H" are stored in the Symbiota database (Gries et al., 2014; Symbiota Collections of Arthropods Network, http://symbiota4.acis.ufl.edu/scan/portal/) under the Hymenoptera Institute Collection (HIC). To search for a specimen in the database, do the following: Under the *Search* tab (upper left of the screen), select *Search Collections*. Deselect all collections, and scroll down the Southeast section, put a check in the box next to *Hymenoptera Institute Collection*, scroll back up and hit the *Search* button (right side of screen). H-numbered specimens are stored with a four-letter prefix (HICH) followed by a six-digit number. Therefore, H369, as it appears in this publication, is stored as HICH000369. To search for this specimen, scroll down to the Specimen Criteria section, type this number in the box next to *Catalog Number* and hit the search button. This displays a page with a summary of the specimen information. Clicking on *Full Record Details* opens a new window with the full specimen record, including all available images.

Each species is diagnosed and described or redescribed, and a plate of images with a chronogram of occurrence is included for each.

SPECIES CONCEPTS

The biological species concept is used with evidence drawn from *COI* sequences, morphology, and host use as indirect evidence for species integrity. *COI* was the primary source of evidence with no particular percent divergence employed as a cut-off. The sequence data were checked against morphological and host-use data, and these corroborated or (rarely) refuted the sequence data.

TAXON SAMPLING

For molecular analyses, we used all *Alabagrus* sequences available to us on the BOLD database from Costa Rica. Once we removed a few sequences that were contaminated in some way, this amounted to 636 sequences. To this, we added 44 *Alabagrus* sequences generated by the Sharkey lab from Costa Rica, Honduras, Mexico, and USA.

MORPHOLOGICAL TERMS

Morphological terms are from Sharkey and Wharton (1997). The reader is advised to search for any morphological term that is not understood on the Hymenoptera Anatomy Ontology website (http://portal.hymao.org/projects/32/public/ontology/; Yoder et al., 2010). To do this, enter the term in the search box, select the best match from the list that pops up, and click on the *show* button.

MUSEUM ACRONYMS

CNCI	Canadian National Collection of Insects, Ottawa, Canada
EMUS	Utah State University, Department of Biology, Entomology Museum, Logan, Utah, USA
HIC	University of Kentucky, Department of Entomology, Hymenoptera Institute Collection, Lexington, Kentucky, USA
INBio	Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
MUCR	Ciudad Universitaria, Universidad de Costa Rica, Museo de Insectos, Costa Rica

DNA EXTRACTION, PCR, AND SEQUENCING

Specimens sequenced in this study are from a variety of sources. Specimens with numbers beginning with DHJPAR, INB, INBIOCRI, or BIOUG were extracted and sequenced for *COI* at the University of Guelph following the methods outlined in Hebert et al. (2004).

Specimens with numbers beginning with the letter "H" were extracted from individual legs with the QIAGEN DNeasy Blood and Tissue Kit using the animal tissue protocol (QIAGEN Inc., Chatsworth, California, USA). The mitochondrial *COI* (~658 bp) gene was amplified with the primer pair LepF1 and LepR1 (Hebert et al., 2004). Polymerase chain reaction (PCR) was conducted using TaKaRa reagents, with each reaction consisting of 1× buffer, 0.3 mM nucleotides, 0.4 μM of each primer, 0.625 U TaKaRa *Ex Taq*, double-distilled water, and 1–3 μL template DNA in a total reaction volume of 25 μL. The thermal cycling protocol had an initial denaturation period at 95 °C for 2.5 min, followed by 40 cycling steps which denatured at 95 °C for 30 s, annealed at 44 °C for 30 s and extended at 68 °C for 45 s, with a final extension step of 72 °C for 7 min. To determine reaction success, PCR products were electrophoresed in 1% agarose stained with ethidium bromide. PCR products were outsourced for Sanger sequencing either by the Advanced Genetic Technologies Center (University of Kentucky, Lexington, Kentucky, USA) or Beckman Coulter Genomics (Danvers, Massachusetts, USA) using labeled dideoxy-nucleotides with ABI 3730, Big-Dye Terminator mix v. 3.0, or with ABI PRISM 3730xl, BigDye Terminator mix v. 3.1 (Applied Biosystems, Foster City, California, USA).

DNA ASSEMBLY AND PHYLOGENETIC ANALYSIS

Bidirectional sequences were aligned and edited using Geneious Pro (v. 6.1.5; Drummond et al., 2009) and multiple alignments were assembled using MAFFT (v. 5; Katoh et al., 2006) using the default settings and refined by eye using MacClade v. 4.08 (Maddison and Maddison, 2005). Maximum likelihood (ML) phylogenetic analyses were conducted on the *COI* data set using Garli (v. 2.01; Zwickl, 2006). The data set consisted of 680 *Alabagrus* OTUs and one sequence from a species of *Pharpa* Sharkey, which was shown to be sister to *Alabagrus* in the most comprehensive molecular agathidine phylogeny to date (Sharkey and Chapman, 2017) for outgroup rooting. The data were partitioned by codon position (three partitions). We applied the most complex model available (GTR+I+G; Rodriguez et al., 1990) to each partition as per recommendations of Huelsenbeck and Rannala (2004) for likelihood-

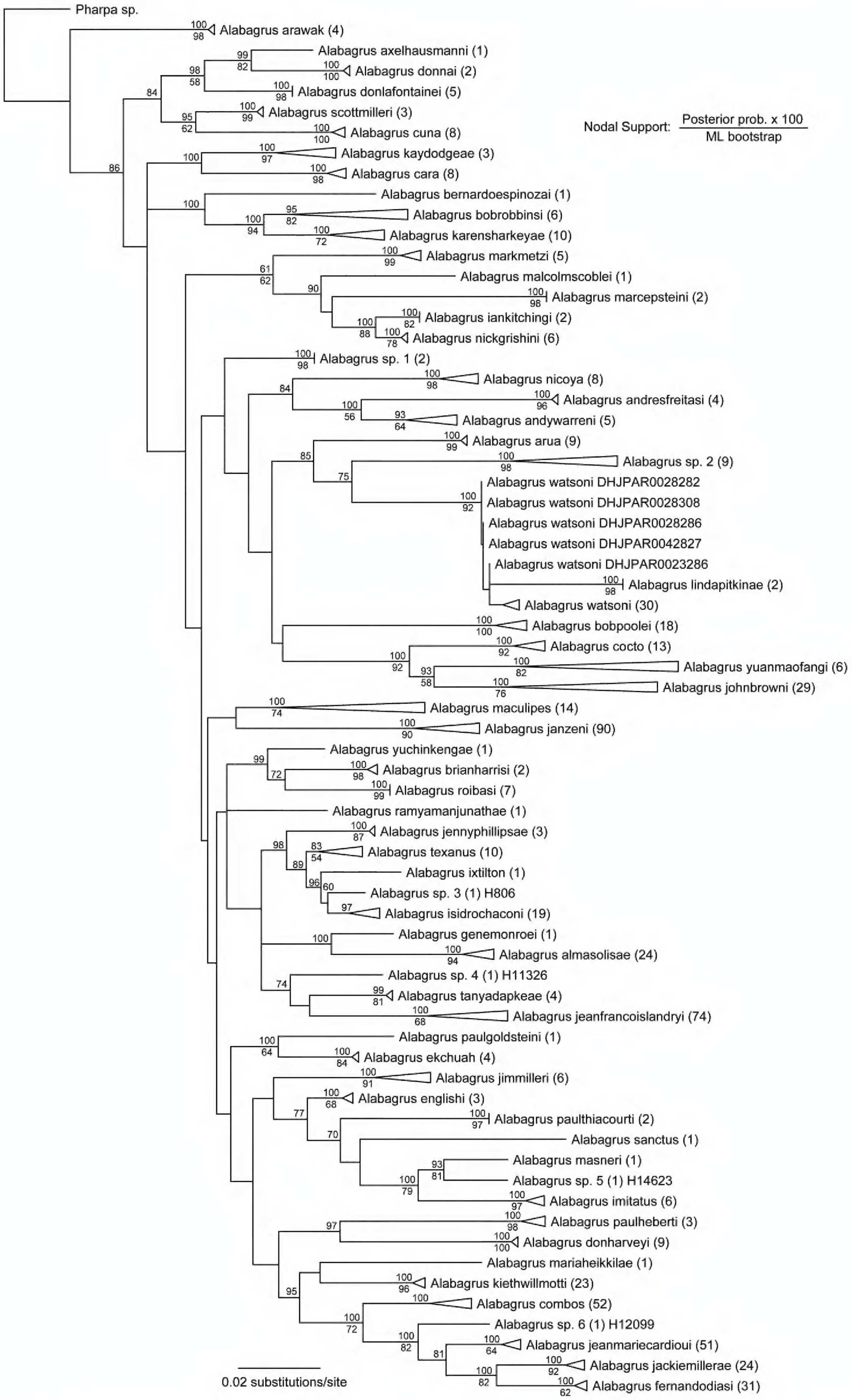

Pharpa sp.
Alabagrus arawak (4)
Alabagrus axelhausmanni (1)
Alabagrus donnai (2)
Alabagrus donlafontainei (5)
Alabagrus scottmilleri (3)
Alabagrus cuna (8)
Alabagrus kaydodgeae (3)
Alabagrus cara (8)
Alabagrus bernardoespinozai (1)
Alabagrus bobrobbinsi (6)
Alabagrus karensharkeyae (10)
Alabagrus markmetzi (5)
Alabagrus malcolmscoblei (1)
Alabagrus marcepsteini (2)
Alabagrus iankitchingi (2)
Alabagrus nickgrishini (6)
Alabagrus sp. 1 (2)
Alabagrus nicoya (8)
Alabagrus andresfreitasi (4)
Alabagrus andywarreni (5)
Alabagrus arua (9)
Alabagrus sp. 2 (9)
Alabagrus watsoni DHJPAR0028282
Alabagrus watsoni DHJPAR0028308
Alabagrus watsoni DHJPAR0028286
Alabagrus watsoni DHJPAR0042827
Alabagrus watsoni DHJPAR0023286
Alabagrus lindapitkinae (2)
Alabagrus watsoni (30)
Alabagrus bobpoolei (18)
Alabagrus cocto (13)
Alabagrus yuanmaofangi (6)
Alabagrus johnbrowni (29)
Alabagrus maculipes (14)
Alabagrus janzeni (90)
Alabagrus yuchinkengae (1)
Alabagrus brianharrisi (2)
Alabagrus roibasi (7)
Alabagrus ramyamanjunathae (1)
Alabagrus jennyphillipsae (3)
Alabagrus texanus (10)
Alabagrus ixtilton (1)
Alabagrus sp. 3 (1) H806
Alabagrus isidrochaconi (19)
Alabagrus genemonroei (1)
Alabagrus almasolisae (24)
Alabagrus sp. 4 (1) H11326
Alabagrus tanyadapkeae (4)
Alabagrus jeanfrancoislandryi (74)
Alabagrus paulgoldsteini (1)
Alabagrus ekchuah (4)
Alabagrus jimmilleri (6)
Alabagrus englishi (3)
Alabagrus paulthiacourti (2)
Alabagrus sanctus (1)
Alabagrus masneri (1)
Alabagrus sp. 5 (1) H14623
Alabagrus imitatus (6)
Alabagrus paulheberti (3)
Alabagrus donharveyi (9)
Alabagrus mariaheikkilae (1)
Alabagrus kiethwillmotti (23)
Alabagrus combos (52)
Alabagrus sp. 6 (1) H12099
Alabagrus jeanmariecardioui (51)
Alabagrus jackiemillerae (24)
Alabagrus fernandodiasi (31)
Nodal Support: Posterior prob. x 100 / ML bootstrap
0.02 substitutions/site

Figure 1 Tree of highest posterior probability from a 10 million–generation Bayes analysis of *COI*. Species are collapsed (when possible) into single terminals (terminal triangles), with the number of OTUs for each collapsed species in parentheses. The length of the triangles represents the branch length from the node to the tip of the longest branch.

based analyses. We conducted a 50-replicate ML search for the tree of highest log-likelihood and a 200-replicate ML bootstrap analysis (Felsenstein, 1985). Both analyses used the default settings.

A Bayesian inference (BI) phylogenetic analysis was also conducted on the *COI* data set with MrBayes (v. 3.1.2; Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). As in the ML analyses, the data were partitioned by codon position. To allow each partition to have its own set of parameter estimates, *revmat*, *tratio*, *statefreq*, *shape*, and *pinvar* were all unlinked during the analyses. To obtain the most accurate branch length estimates possible, the option *prset ratepr=variable* (which assigns a separate branch length parameter for each partition) was employed as per the recommendations of Marshall et al. (2006). A temperature (t) setting of 0.01 was used because there was insufficient chain swapping in a pilot run with the default value t=0.1. With t=0.01, the average chain swapping value was 55%. Two independent, simultaneous BI searches were run for 10 million generations, saving a tree every 1000 generations, with four search chains each. The average standard deviation of split frequencies was 0.0235 at the completion of 10 million generations. The log-likelihood values of the chains in both analyses plateaued just above –10,000 by 3 million generations and did not go any lower by the completion of the run. The likelihood of best state for the "cold" chain of run 1 was –9911.85 and that for the "cold" chain of run 2 was –9912.76. The 5000 post–burn-in trees from each run (10,000 total), using a 50% burn-in were used to calculate the majority rule consensus tree using PAUP* (v. 4.0β10; Swofford, 2003). The data set analyzed herein, including the MrBayes command block and Garli configuration files are available from the authors upon request.

RESULTS

PHYLOGENETIC TREES

The tree of highest posterior probability from the Bayesian analysis with species collapsed into single terminals (when possible) is shown in Figure 1, including nodal support values from the Bayes and ML analyses. We also present four supplemental trees: Bayesian tree of highest posterior probability (Supplemental Figure 1), Bayesian consensus tree (Supplemental Figure 2), tree of highest log-likelihood (Supplemental Figure 3), and ML bootstrap consensus tree (Supplemental Figure 4).

PHYLOGENETIC CONSIDERATIONS

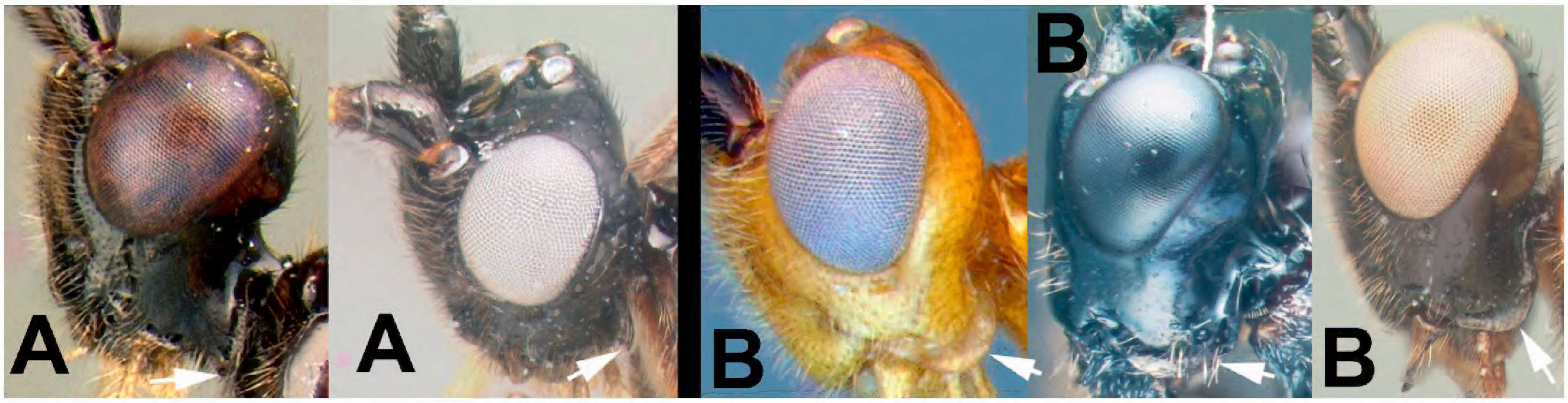
The phylogenetic tree in Figure 1 does not have well-supported basal branches. Its primary purpose was as a source of evidence to delineate species. Nonetheless, several lineages are worth noting. *Alabagrus fernandodiasi*, *A. jackiemillerae*, and *A. jeanmariecadioui* form a clade, and all members are similar in color and morphology (BIPP=81, MLBS<50). None are represented by males, which is unusual considering each is represented by 24 or more specimens. It may represent a parthenogenetic clade. Three species, *Alabagrus donlafontainei*, *A. cuna*, and *A. scottmilleri*, are distinctly sexually dichromatic, and all are found in a clade composed of five species (BIP=84, MLBS<50). One of the other species, *A. axelhausmanni*, is represented by a male only as the holotype, and the other member of the clade, *A. donnai*, have males that are darker (orange rather than yellow) than females (BIPP=99, MLBS=82). Overall it is common to have structural sexual dimorphism in members of *Alabagrus*. In particular, sculpture of the propodeum is often much more pronounced in males than females.

KEY TO COSTA RICAN *ALABAGRUS*

If you know the species of the host caterpillar it might be best to use the search function on electronic versions of this publication and find the species of *Alabagrus* that is (are) on the host, and check your specimen against the images and description. It is doubtful that this key will be very useful outside of Costa Rica and adjacent countries.

1A. Gena right angled or acute posteroventrally 2

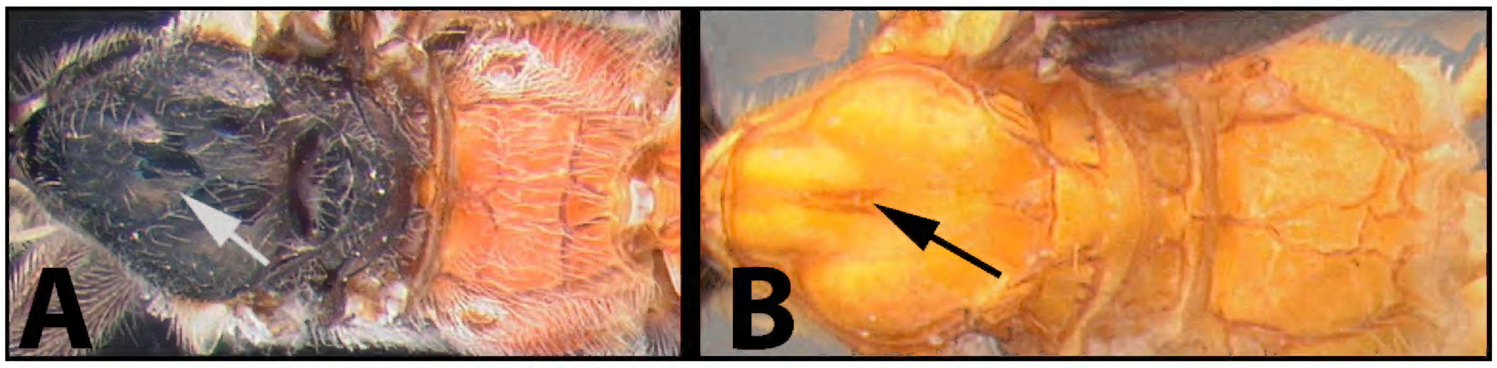
1B. Gena rounded or with an obtuse angle posteroventrally 78



Couplet 1

2(1)A. Mesoscutum mostly or entirely melanic.......3

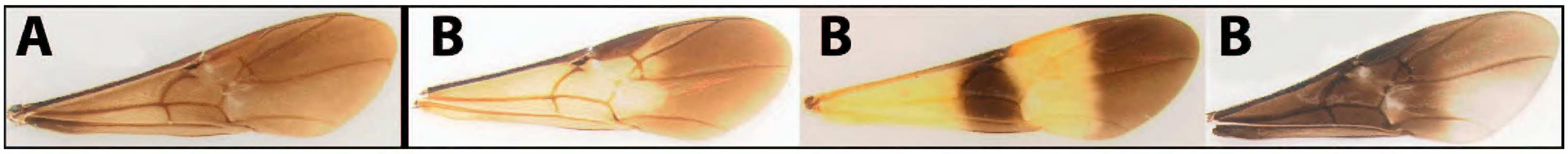
2(1)B. Mesoscutum mostly or entirely pale 63



Couplet 2

3(2)A. Forewing almost entirely infuscate, ignore small clear patches posteriad stigma 4

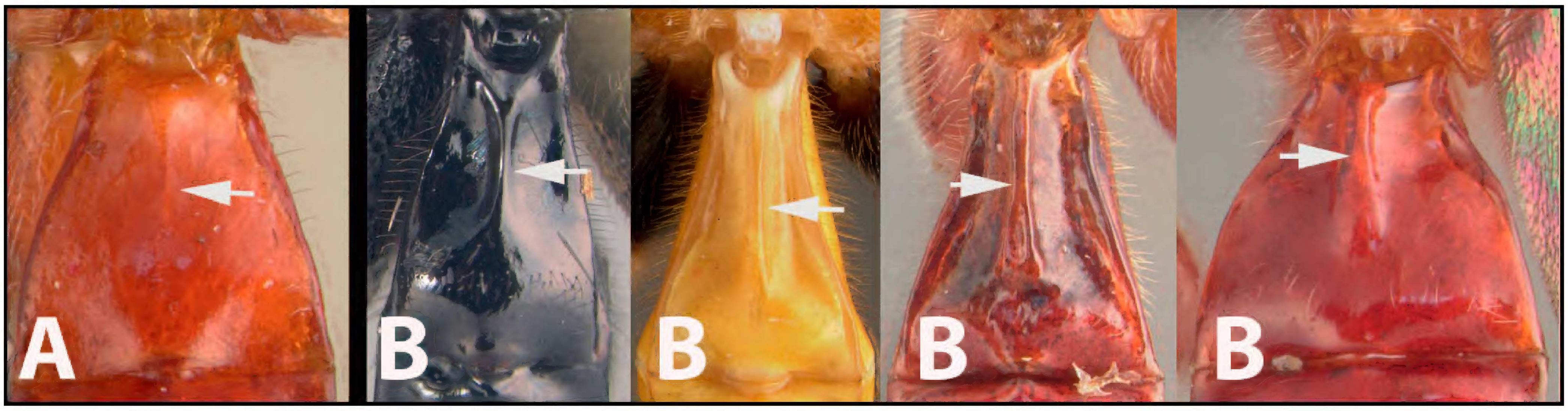
3(2)B. Forewing patterned with large clear, white, or yellow areas.......18



Couplet 3

4(3)A. First tergum varying from weakly convex to with a rounded longitudinal bulge.......5

4(3)B. First tergum with well-defined median longitudinal carina 14

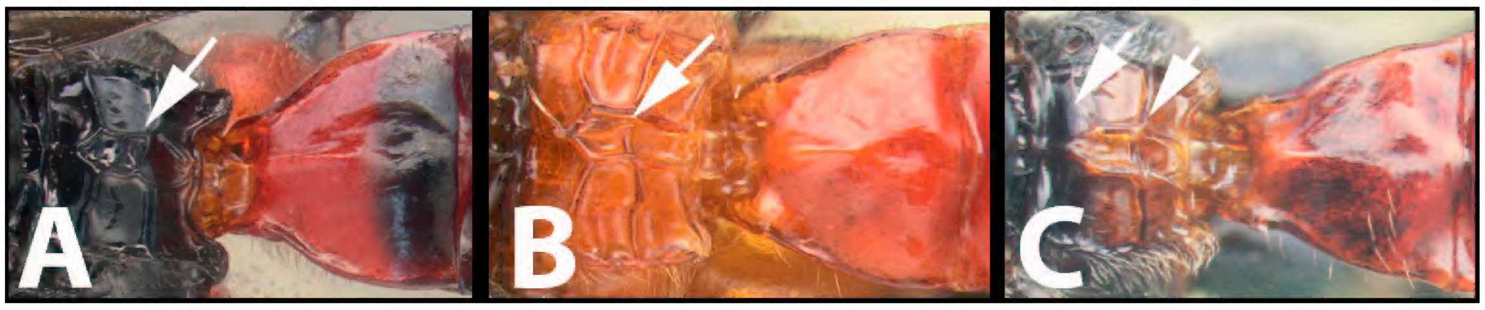


Couplet 4

5(4)A. Propodeum melanic 6

5(4)B. Propodeum pale 8

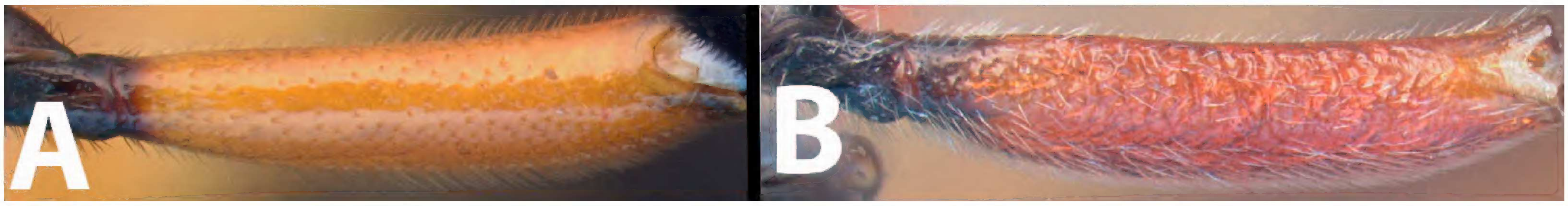
5(4)C. Propodeum melanic anteriorly, pale posteriorly ....*A. combos*



Couplet 5

6(5)A. Hind femur with weak sparse punctures ventrally, little or no more heavily sculptured than dorsal surface 7

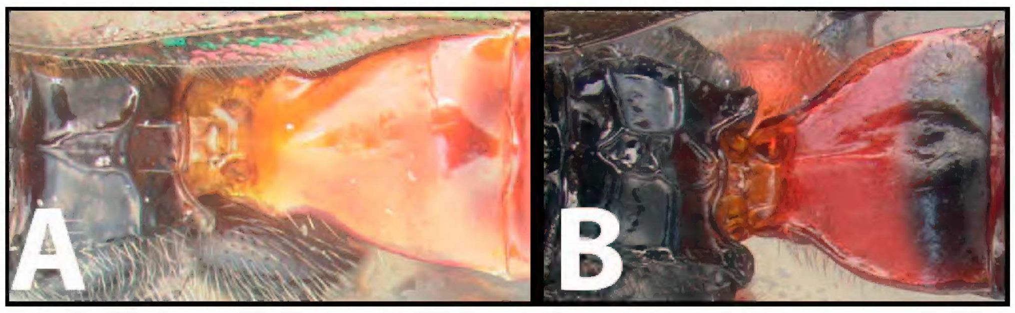
6(5)B. Hind femur heavily sculptured ventrally with aciculations or rugosities, distinctly more heavily sculptured than dorsal surface .... ***A. donharveyi* n. sp.**



Couplet 6

7(6)A. Median tergite 1 narrower .... ***A. leedyeri* n. sp.**

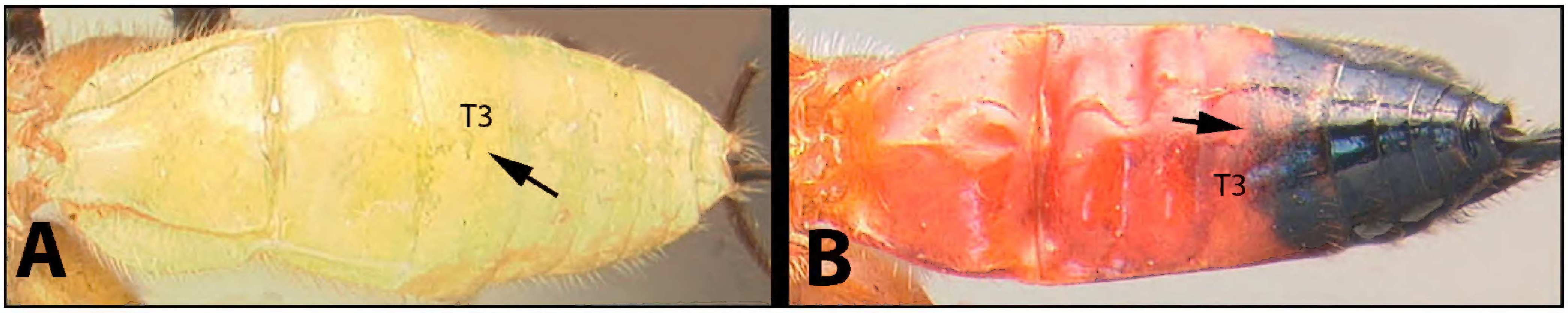
7(6)B. Median tergite 1 wider .... ***A. johnsharkeyi* n. sp.**



Couplet 7

8(5)A. Median tergite 3 pale 9

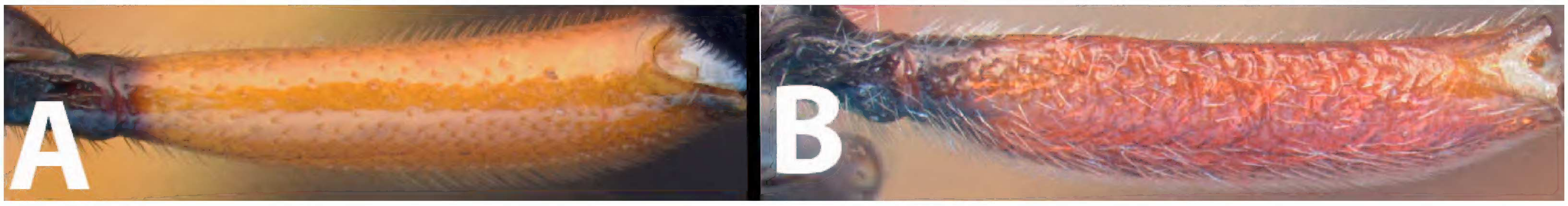
8(5)B. Median tergite 3 pale anteriorly, melanic posteriorly .... *A. watsoni*



Couplet 8

9(8)A. Hind femur with weak sparse punctures ventrally, little or no more heavily sculptured than dorsal surface 10

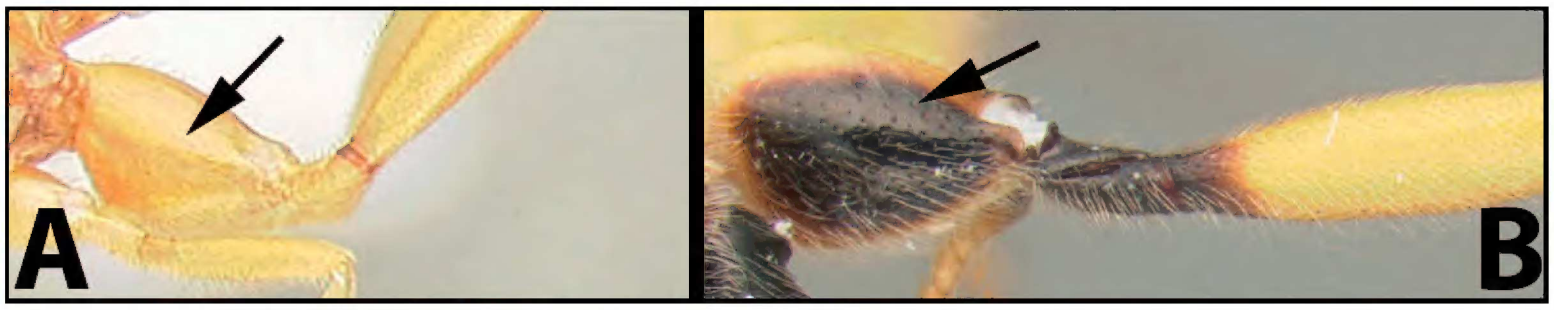
9(8)B. Hind femur heavily sculptured ventrally with aciculations or rugosities, distinctly more heavily sculptured than dorsal surface 12



Couplet 9

10(9)A. Hind coxa entirely pale 11

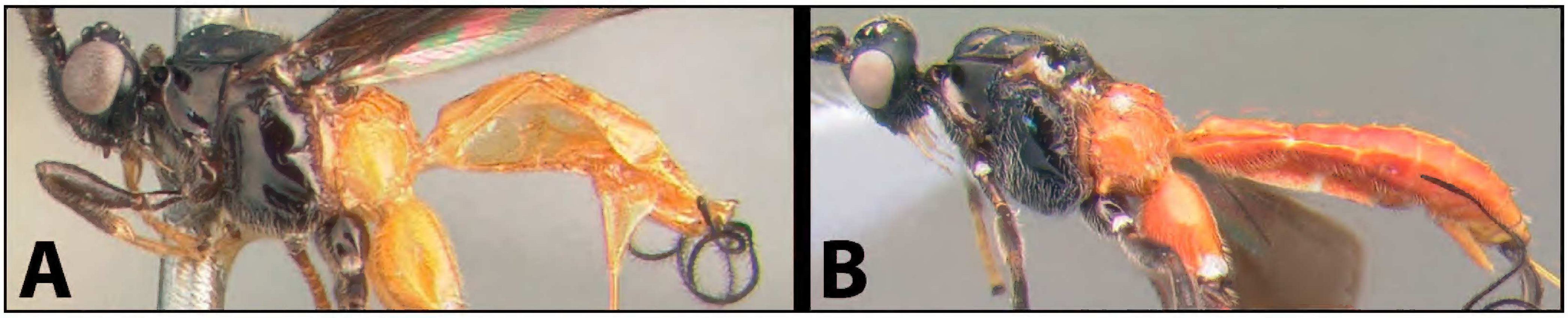
10(9)B. Hind coxa pale medially with a large melanic patch or vertical stripe laterally .... *A. sarapiqui*



Couplet 10

11(10)A. Body black and yellow .... *A. donnai*

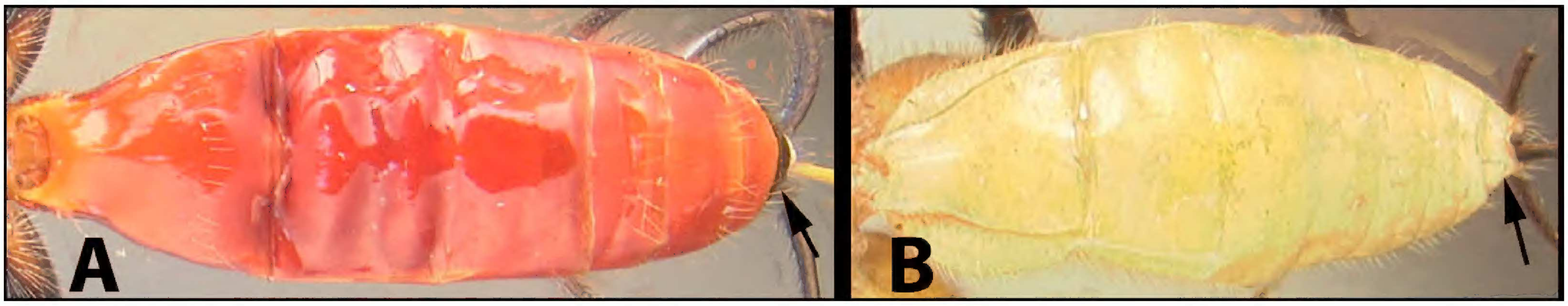
11(10)B. Body black and red to black and orange .... ***A. jimmilleri* n. sp.**



Couplet 11

12(9)A. Penultimate metasomal tergum (often more terga) melanic .... *A. combos*

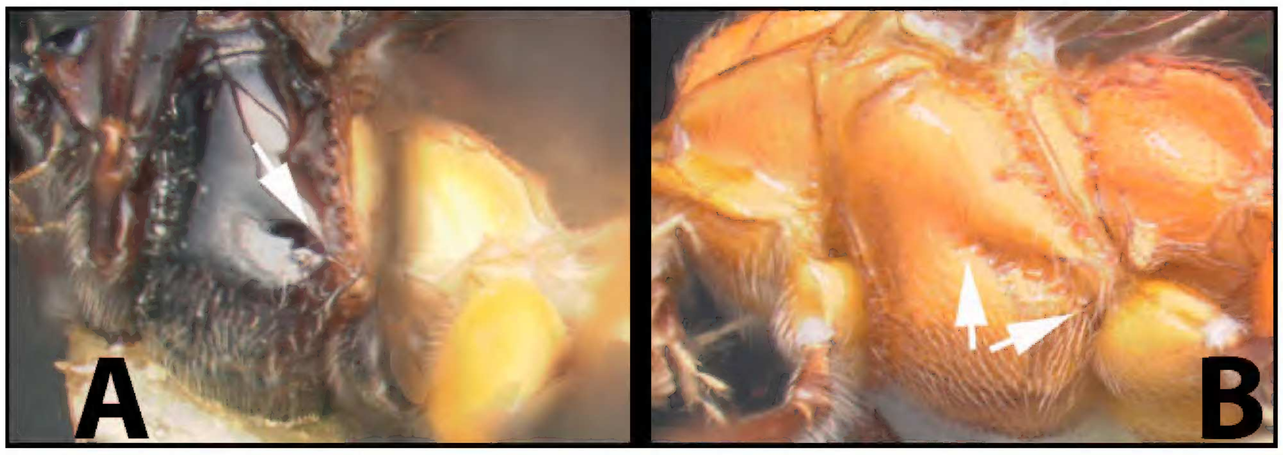
12(9)B. Penultimate metasomal tergum pale, reddish orange to yellow 13



Couplet 12

13(12)A. Precoxal sulcus with one or several distinct foveae posteroventrally, with or without a smooth groove extending anteriorly; pale parts of body yellow .... *A. donnai*

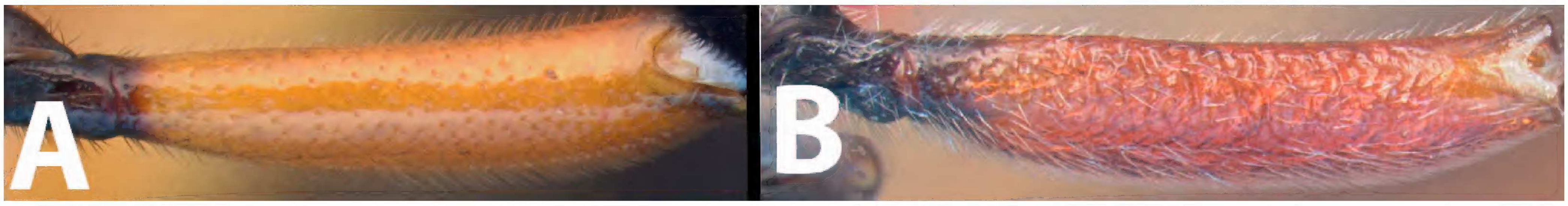
13(12)B. Precoxal sulcus distinct and foveolate ½ or more length of mesopleuron; pale parts of body orange........ *A. arawak*



Couplet 13

14(4)A. Hind femur with weak sparse punctures ventrally, little or no more heavily sculptured than dorsal surface........ 15

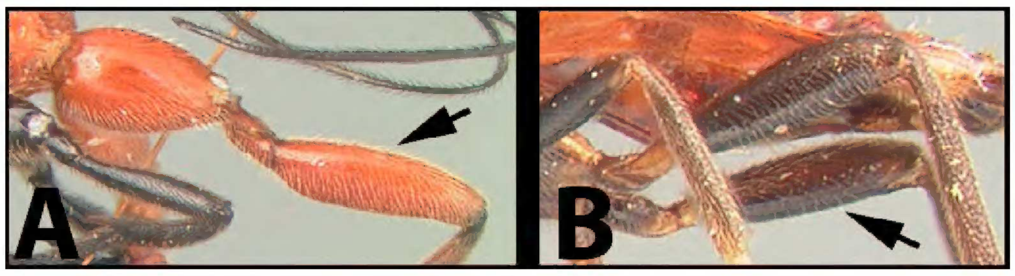
14(4)B. Hind femur heavily sculptured ventrally with aciculations or rugosities, distinctly more heavily sculptured than dorsal surface .... ***A. axelhausmanni* n. sp.**



Couplet 14

15(14)A. Hind femur mostly or entirely pale .... ***A. bernardoespinozai* n. sp.**

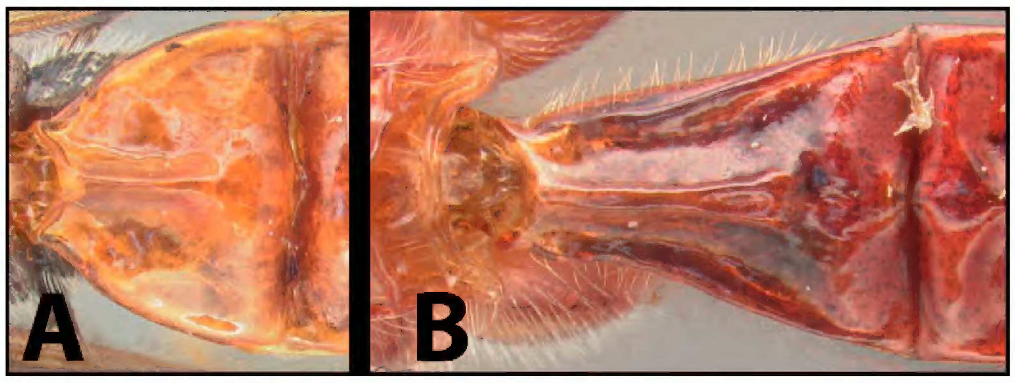
15(14)B. Hind femur mostly or entirely melanic 16



Couplet 15

16(15)A. Median tergite 1 wider than long. .... *A. miqa*

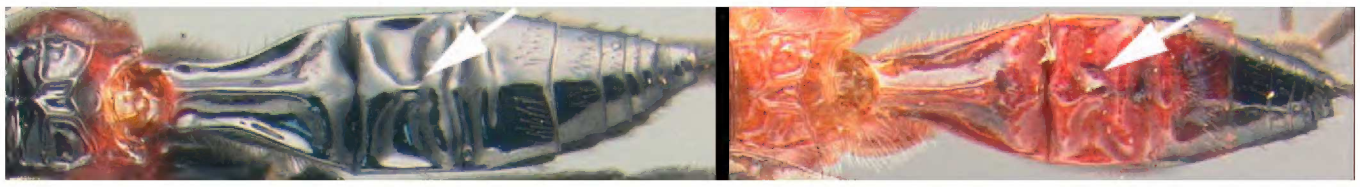
16(15)B. Median tergite 1 longer than wide........ 17



Couplet 16

17(16,31,32)A. Median tergite 2 black .... ***A. bobrobbinsi* n. sp.**

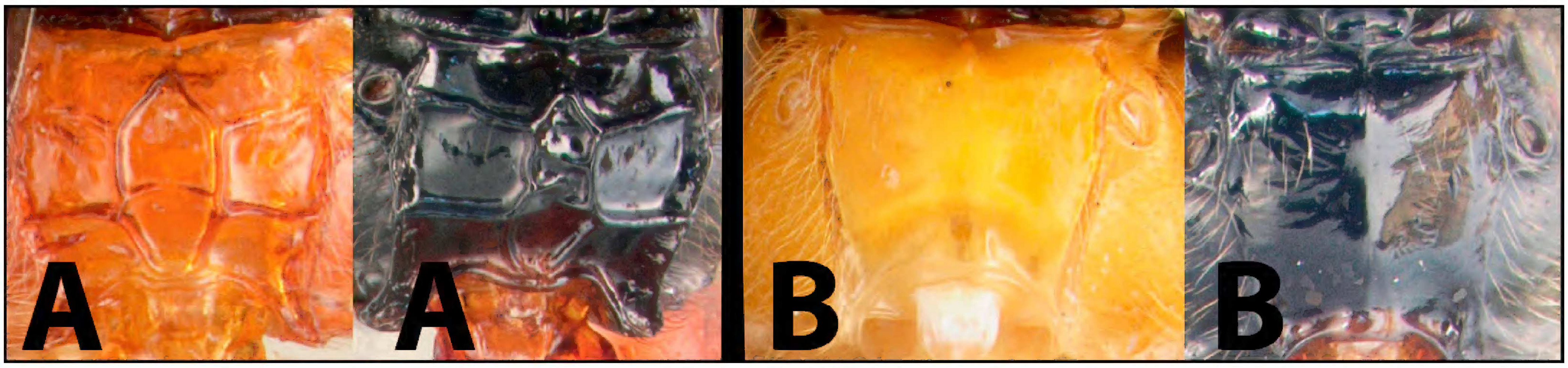
17(16,31,32)B. Median tergite 2 red/orange .... ***A. karensharkeyae* n. sp.**



Couplet 17

18(3)A. Propodeum areolate, with at least one closed areola 19

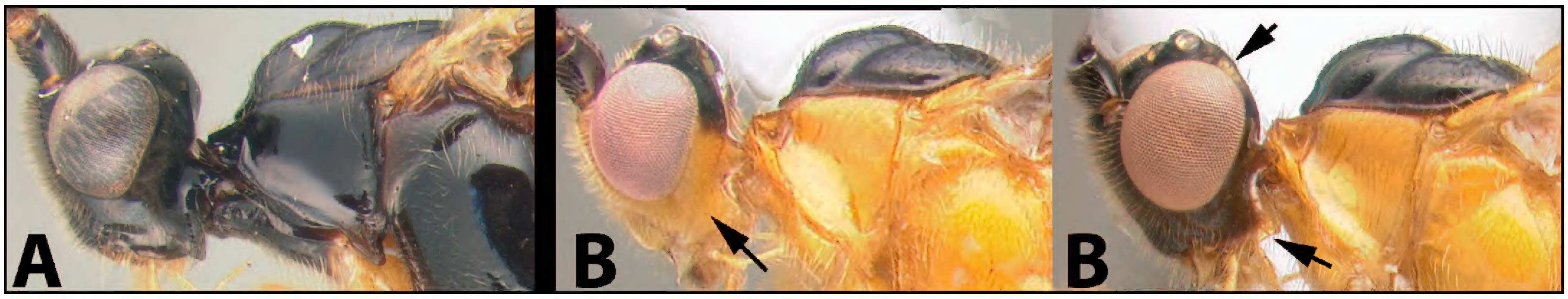
18(3)B. Propodeum lacking complete areolae, usually mostly or completely smooth 41



Couplet 18

19(18)A. Head entirely melanic 20

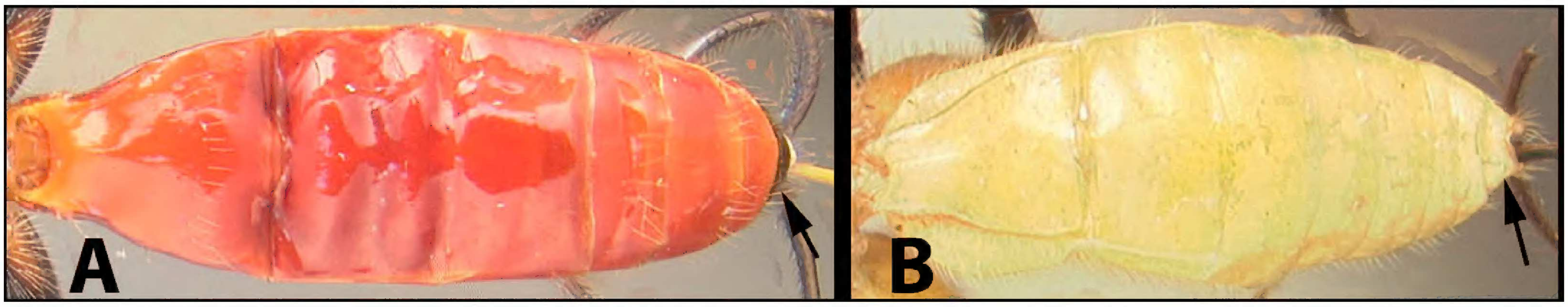
19(18)B. Head with at least some traces of pale color .... ***A. kaydodgeae* n. sp.**



Couplet 19

20(19)A. Penultimate metasomal tergum (or more) melanic 21

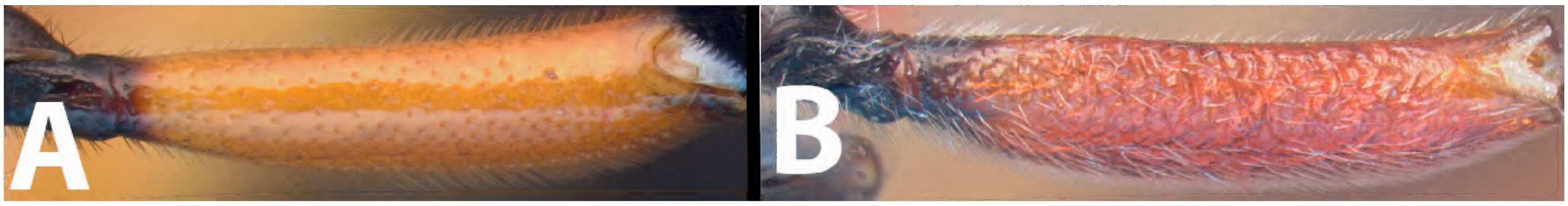
20(19)B. Penultimate metasomal tergum pale, reddish orange to yellow .... ***A. paulsharkeyi* n. sp.**



Couplet 20

21(20)A. Hind femur with weak sparse punctures ventrally, little or no more heavily sculptured than dorsal surface....................................22

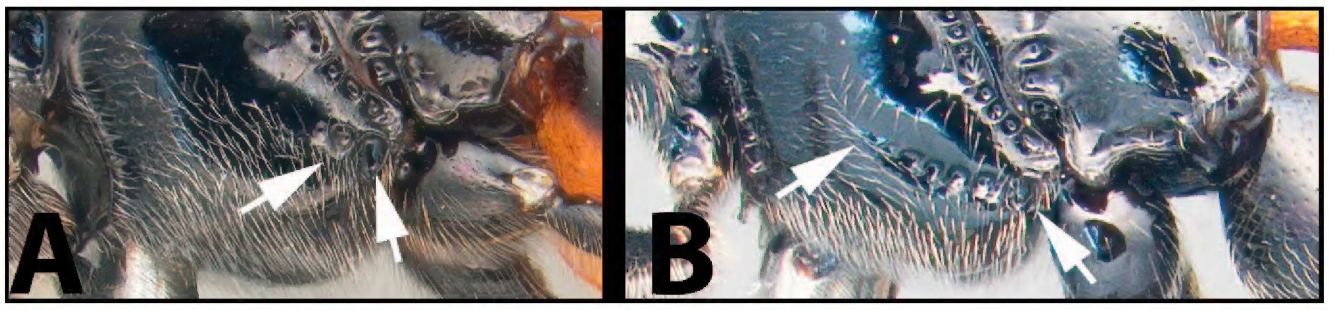
21(20)B. Hind femur heavily sculptured ventrally with aciculations or rugosities, distinctly more heavily sculptured than dorsal surface 38



Couplet 21

22(21)A. Precoxal sulcus with one or several foveae posteroventrally, with or without a smooth groove extending anteriorly........................23

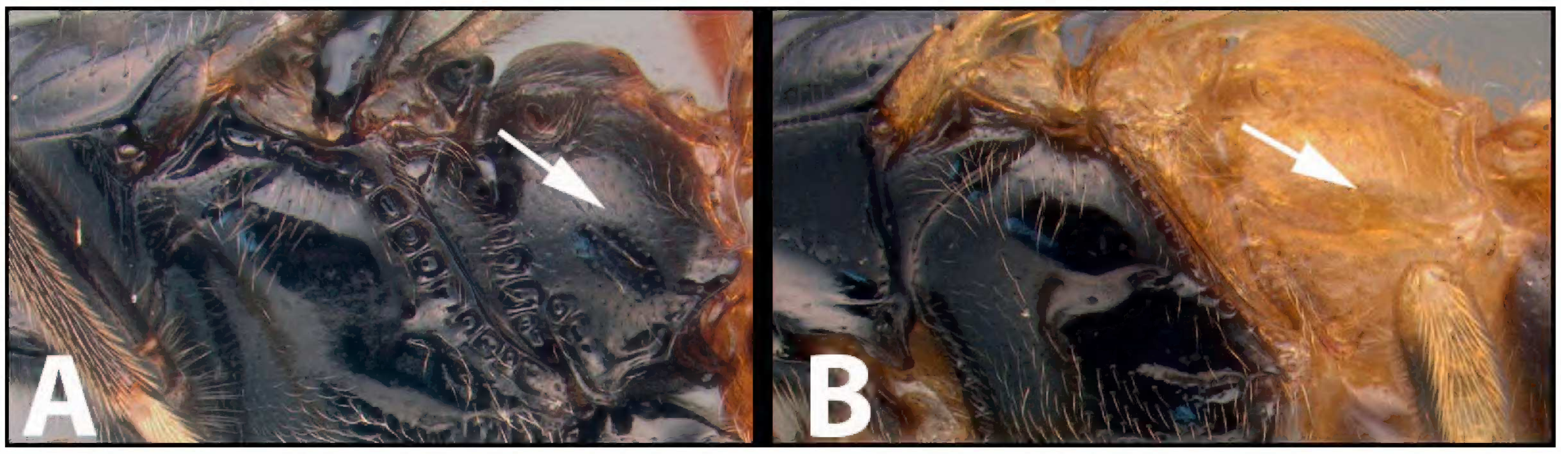
22(21)B. Precoxal sulcus longer, distinct and foveolate ½ or more length of mesopleuron 33



Couplet 22

23(22)A. Metapleuron mostly or entirely melanic 24

23(22)B. Metapleuron mostly or entirely pale 30

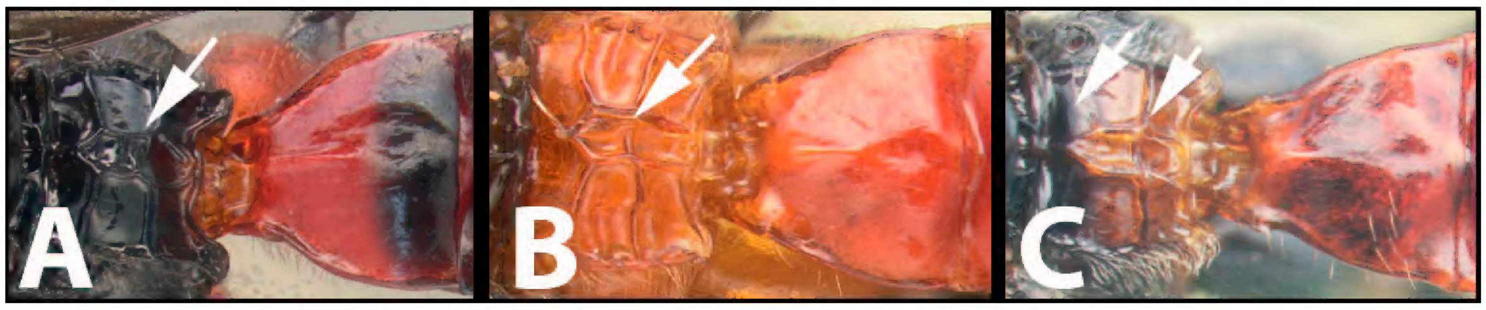


Couplet 23

24(23)A. Propodeum melanic 25

24(23)B. Propodeum pale 28

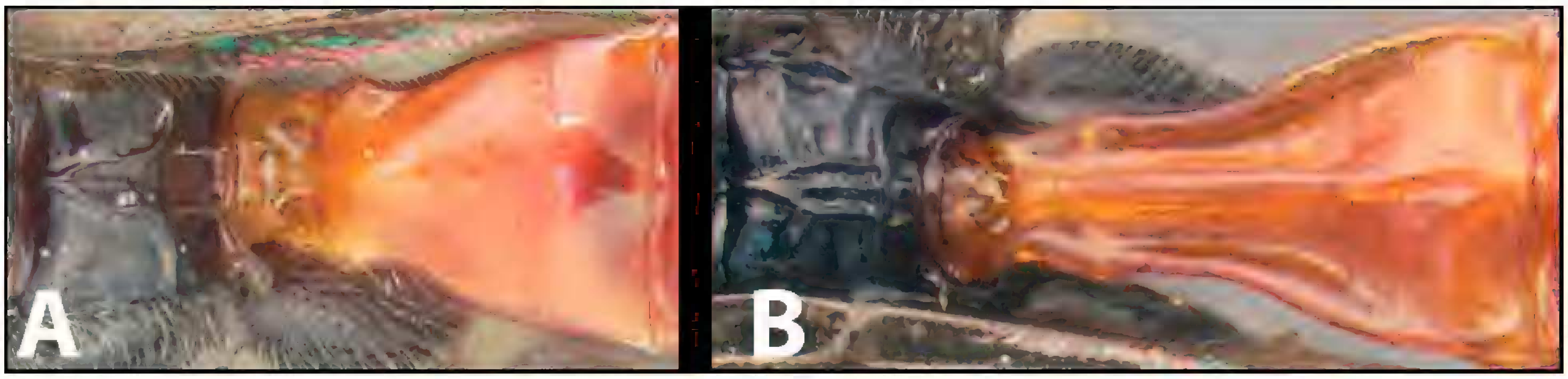
24(23)C. Propodeum melanic anteriorly, pale posteriorly ....***A. almasolisae* n. sp.**



Couplet 24

25(24)A. First tergum varying from weakly convex to with a rounded longitudinal bulge 26

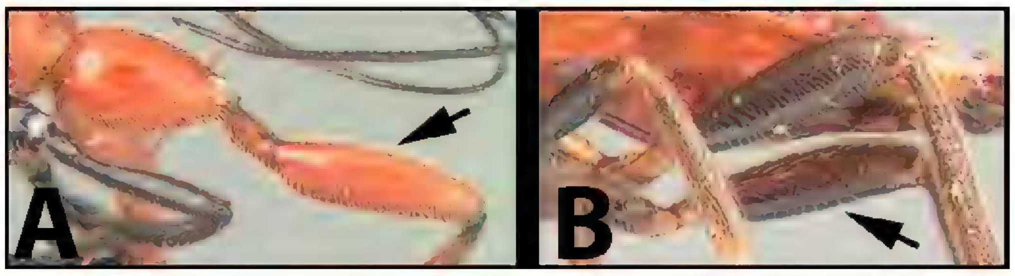
25(24)B. First tergum with well-defined median longitudinal carina 27



Couplet 25

26(25)A. Hind femur mostly or entirely pale .... ***A. almasolisae* n. sp.** males

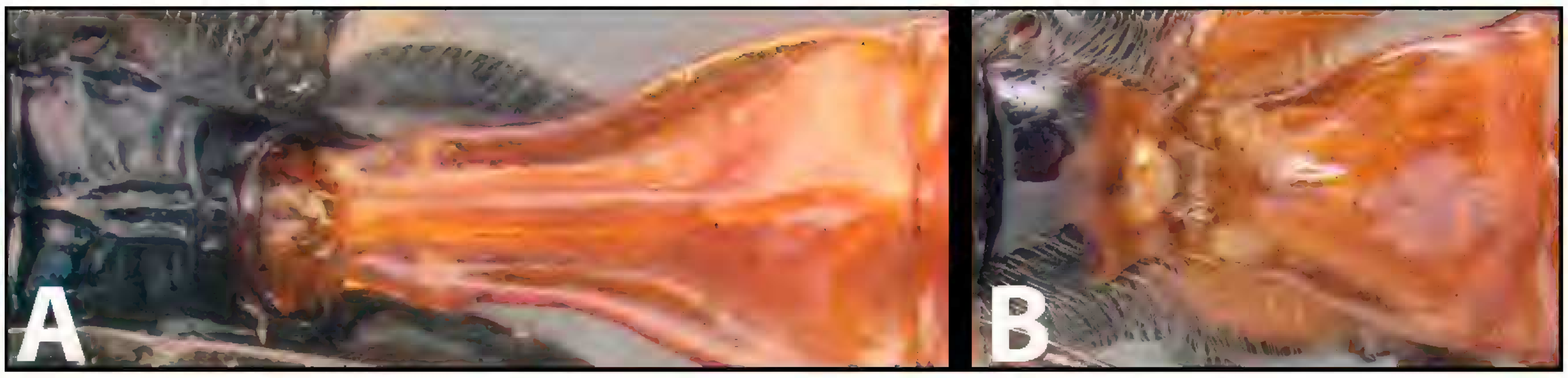
26(25)B. Hind femur mostly or entirely melanic .... ***A. leedyeri* n. sp.**



Couplet 26

27(25)A. Median tergite 1 narrower with a stronger median ridge .... ***A. bobpoolei* n. sp.** males

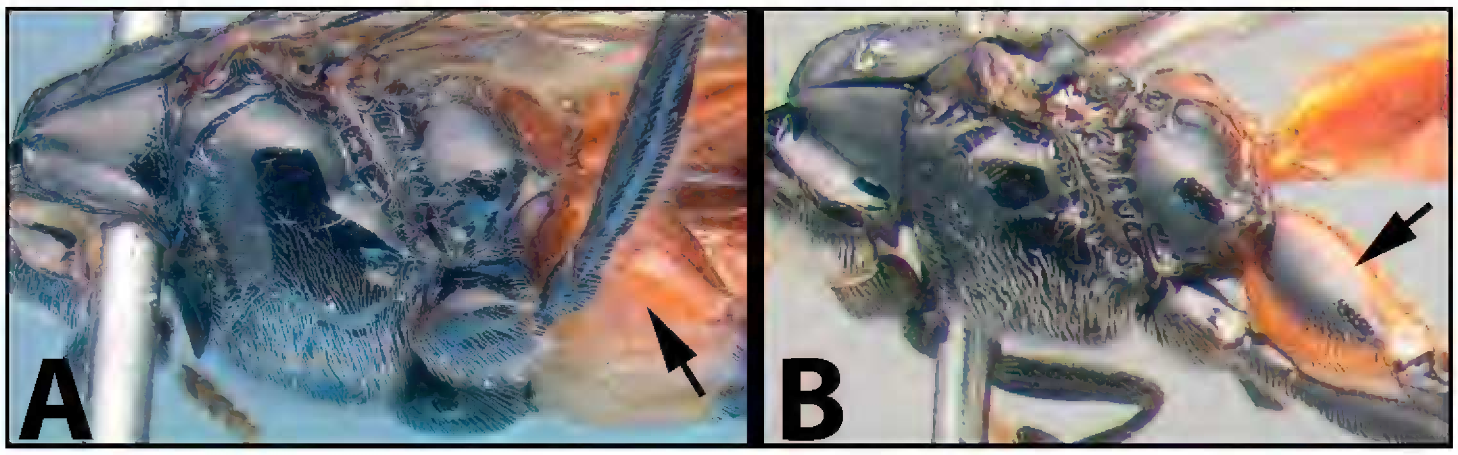
27(25)B. Median tergite wider with a weak longitudinal ridge or anteromedial bulge .... ***A. almasolisae* n. sp.** males



Couplet 27

28(24)A. Hind coxa entirely pale; third tergum with deep transverse depression..***A. tommyersi* n. sp.**

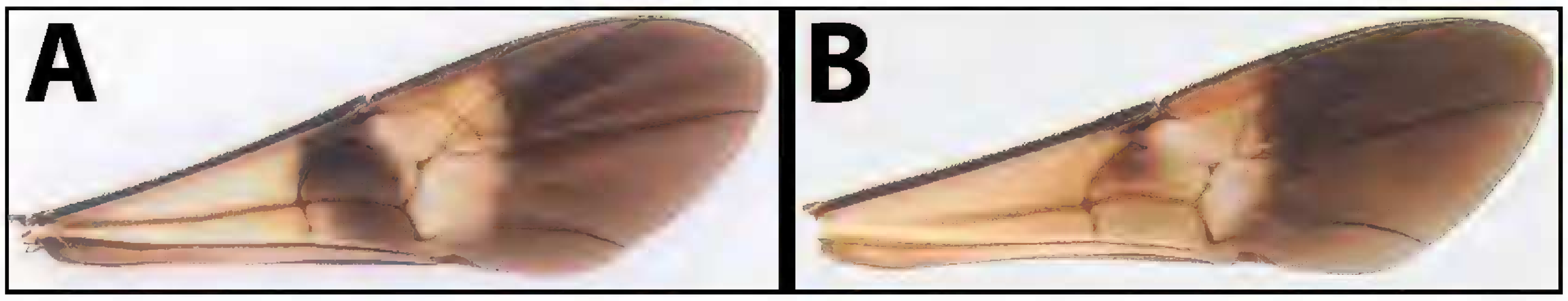
28(24)B. Hind coxa mostly pale with a vertical melanic stripe; third tergum lacking transverse depression or depression barely indicated ...29



Couplet 28

29(28)A. Forewing with two distinct pale areas, one basally and one below stigma ....***A. almasolisae* n. sp.** males

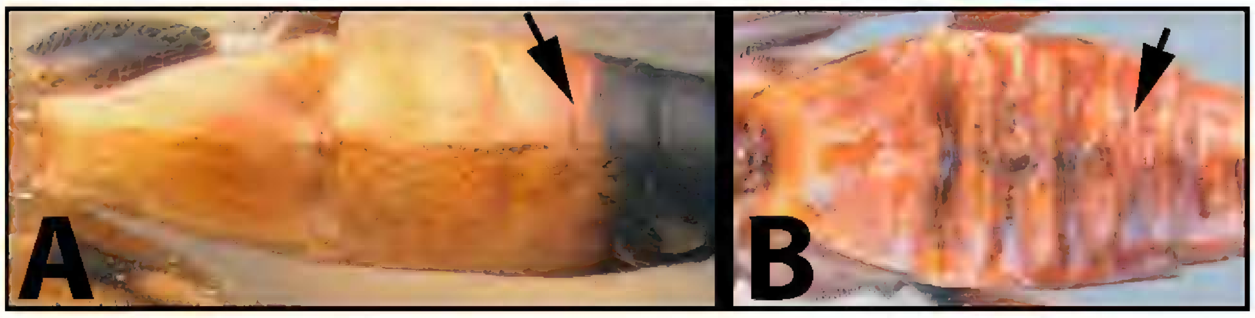
29(28)B. Forewing lacking two distinct pale areas; base of the wing pale with some melanic color behind parastigma..***A. marcepsteini* n. sp.**



Couplet 29

30(23)A. Third tergum lacking transverse depression or depression barely indicated...31

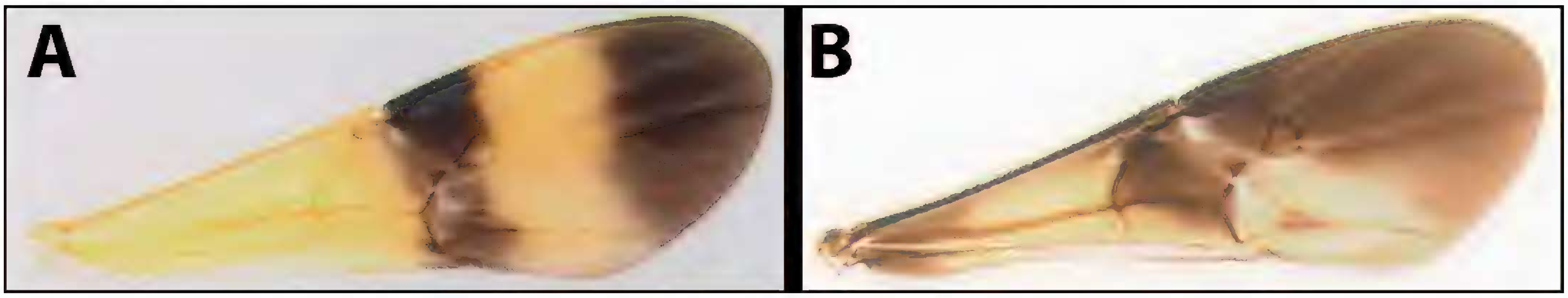
30(23)B. Third tergum with deep transverse depression..32



Couplet 30

31(30)A. Forewing banded from base: yellow, melanic, yellow, melanic...***A. genemonroei* n. sp.**

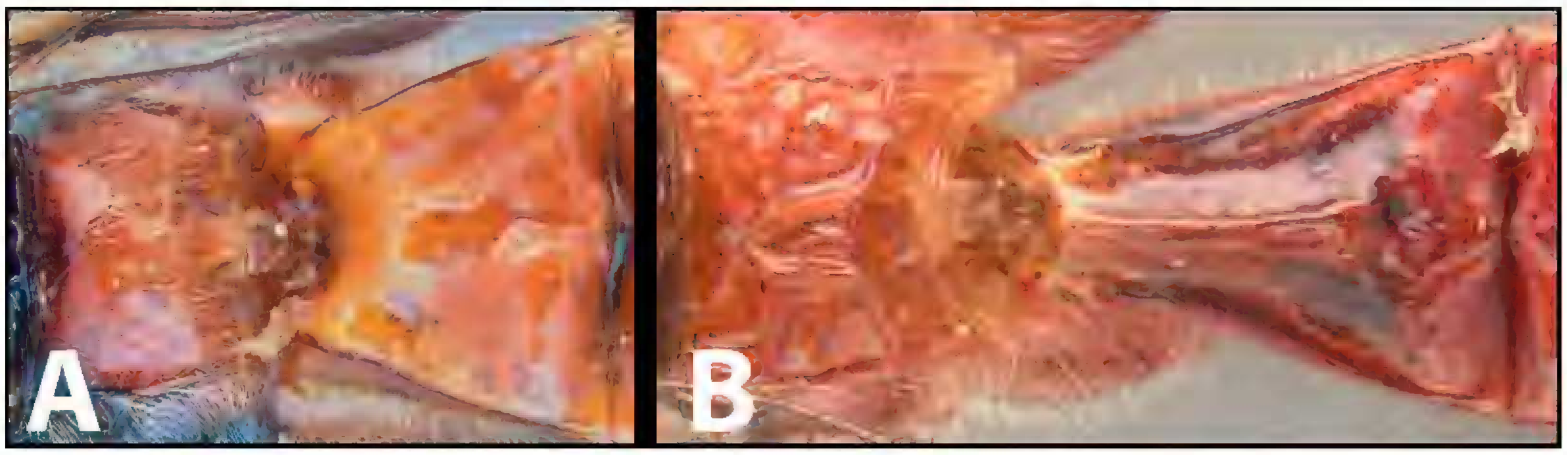
31(30)B. Forewing mostly or entirely infuscate often with pale patches that do not form discrete bands..17



Couplet 31

32(30)A. First tergum varying from weakly convex to with a rounded longitudinal bulge .... ***A. tommyersi* n. sp.**

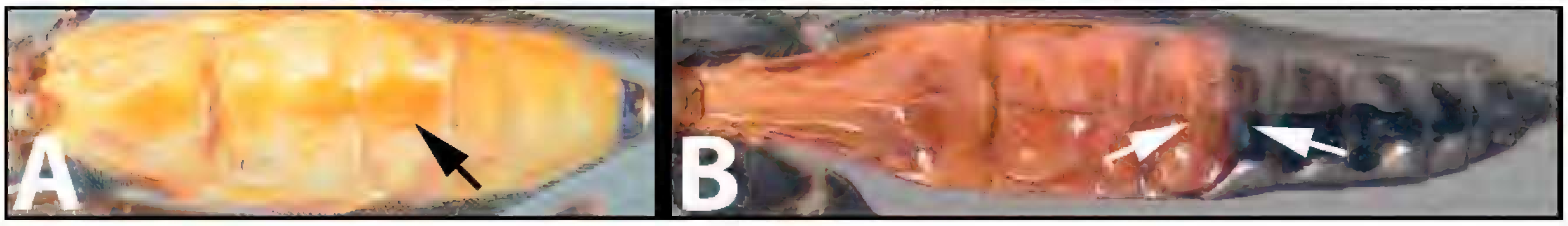
32(30)B. First tergum with well-defined median longitudinal carina 17



Couplet 32

33(22)A. Median tergite 3 pale 34

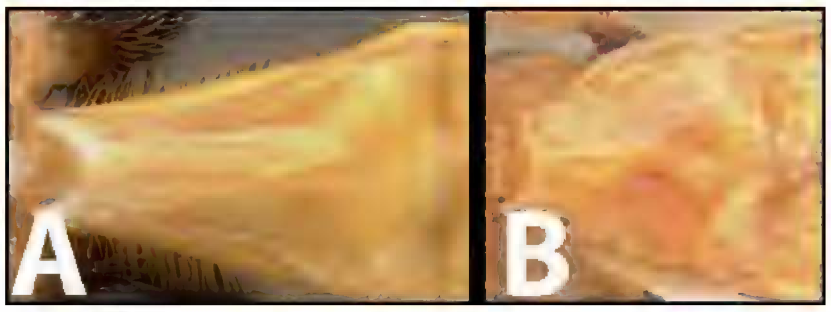
33(22)B. Median tergite 3 pale anteriorly, melanic posteriorly 36



Couplet 33

34(33)A. Median tergite 1 narrower with a stronger median ridge 35

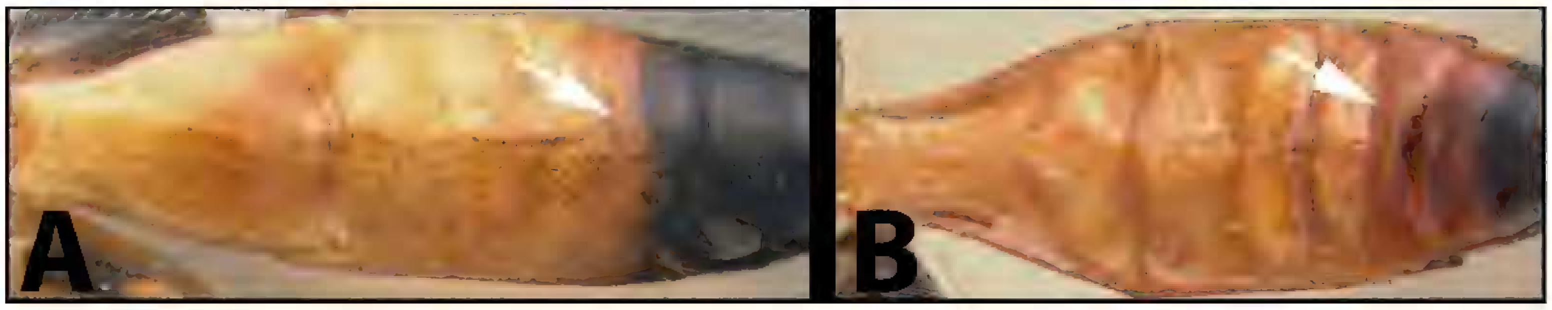
34(33)B. Median tergite wider with a weak longitudinal ridge or anteromedial bulge .... ***A. andywarreni* n. sp.** males



Couplet 34

35(34)A. Third tergum lacking transverse depression or depression barely indicated .... ***A. genemonroei* n. sp.**

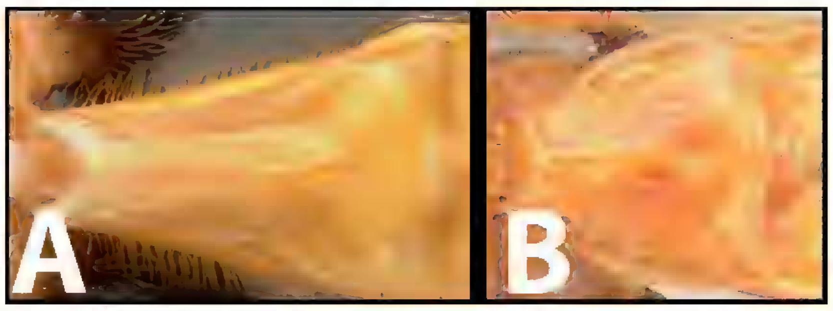
35(34)B. Third tergum with deep transverse depression .... *A. janzeni* males



Couplet 35

36(33)A. First tergum with well-defined median longitudinal carina 37

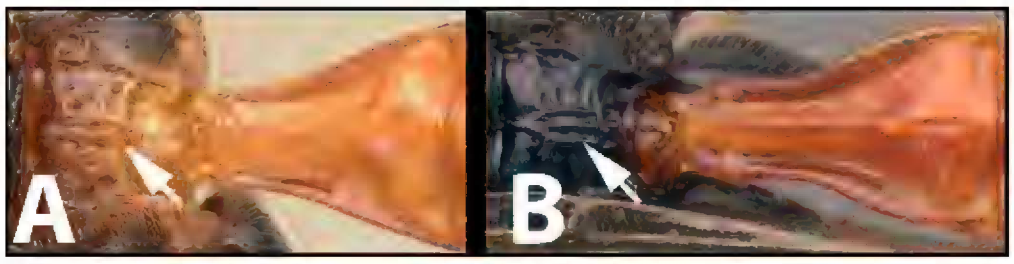
36(33)B. First tergum varying from weakly convex to with a rounded longitudinal bulge .... ***A. lindapitkinae* n. sp.**



Couplet 36

37(36)A. Propodeum mostly or entirely pale .... *A. janzeni* males

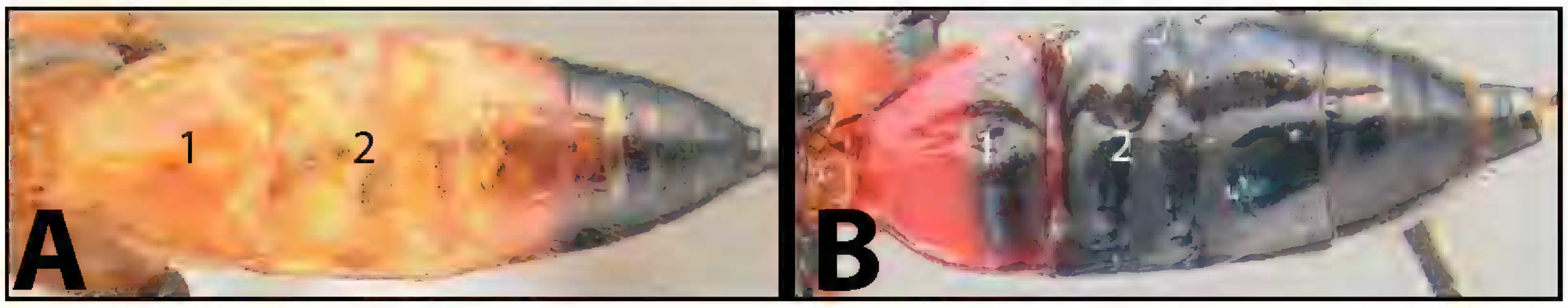
37(36)B. Propodeum entirely melanic .... ***A. bobpoolei* n. sp.** males



Couplet 37

38(21)A. Median tergite 1 pale; median tergite 2 pale 39

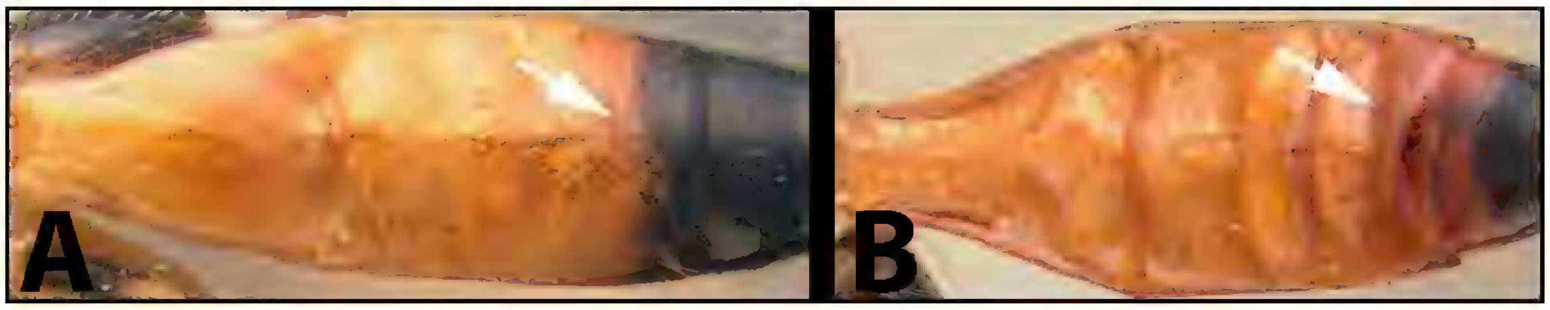
38(21)B. Median tergite 1 partly melanic but pale at base; median tergite 2 melanic .... ***A. donharveyi* n. sp.**



Couplet 38

39(38)A. Third tergum lacking transverse depression or depression barely indicated 40

39(38)B. Third tergum with deep transverse depression .... *A. janzeni* males

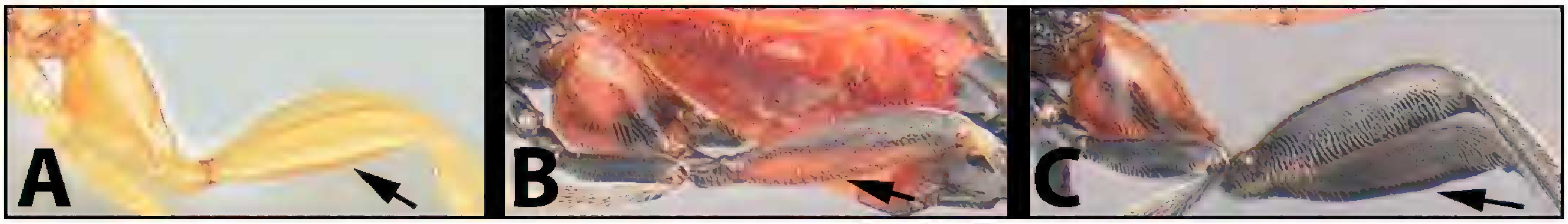


Couplet 39

40(39)A. Hind femur entirely pale........ ***A. andywarreni* n. sp.** males

40(39)B. Hind femur melanic dorsally, pale ventrally........ ***A. paulgoldsteini* n. sp.**

40(39)C. Hind femur entirely melanic, sometimes with a hint of reddish color ventrally but much darker than *A. paulgoldsteini* .... ***A. ramyamanjunathae* n. sp.**

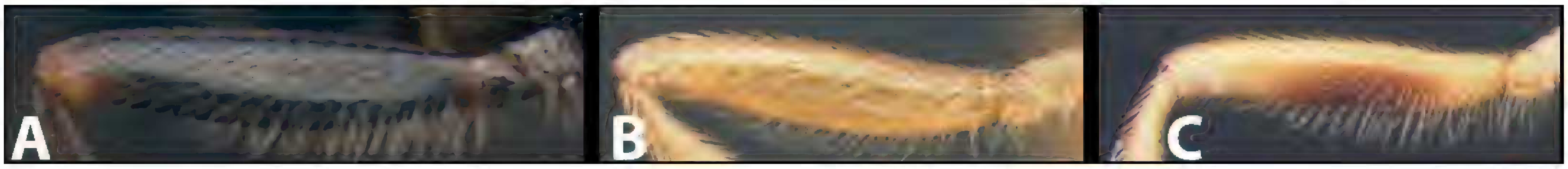


Couplet 40

41(18)A. Forefemur entirely melanic or only with a spot of pale color apically 42

41(18)B. Forefemur entirely pale 57

41(18)C. Forefemur melanic bicolored, pale and melanic 61



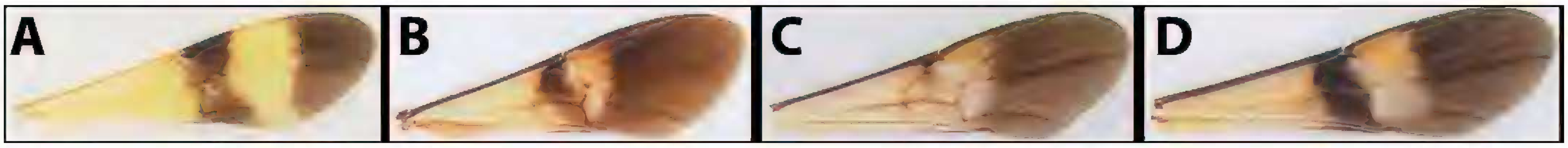
Couplet 41

42(41)A. Forewing with two distinct yellow bands, one basal to and the other apical to stigma 43

42(41)B. Forewing with two yellow bands, one distinct basal band and a weaker triangular band directly below (posterior to) stigma 46

42(41)C. Forewing lacking two distinct bands; pale basally to near level of apex of stigma with a small darkening near parastigma 50

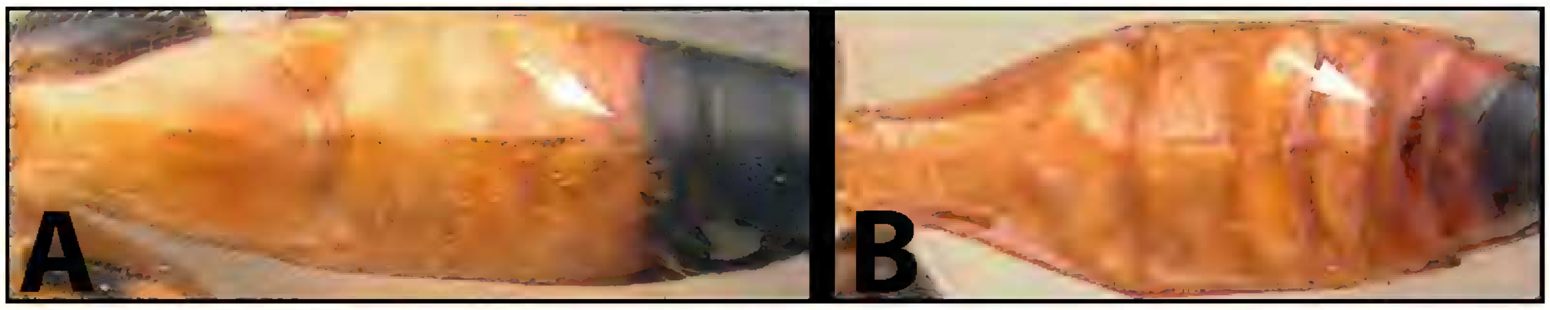
42(41)D. Forewing with two distinct yellow bands, one basal to and the other directly below (posterior to) stigma 54



Couplet 42

43(42)A. Third tergum lacking transverse depression or depression barely indicated........44

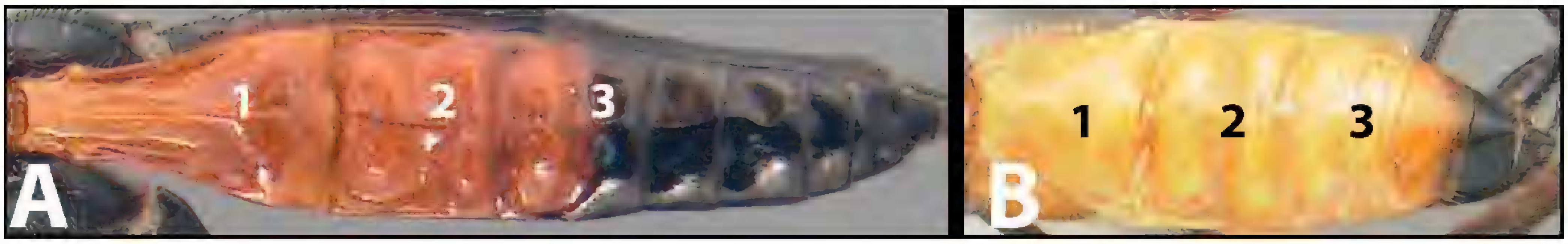
43(42)B. Third tergum with deep transverse depression........45



Couplet 43

44(43)A. Median tergite 3 partly or entirely melanic .... ***A. bobpoolei* n. sp.** females

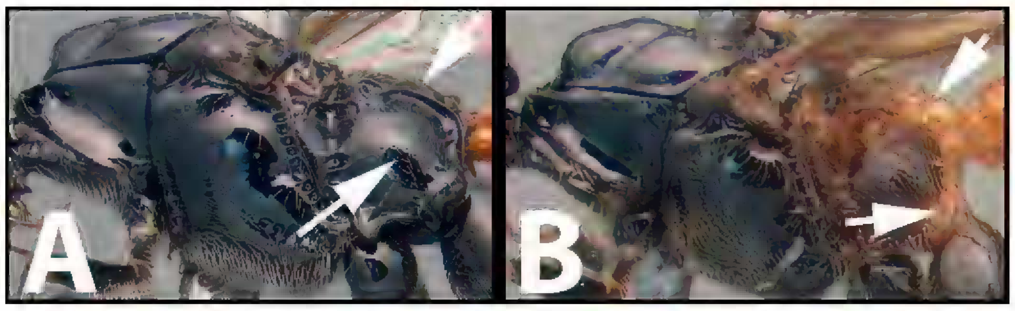
44(43)B. Median tergite 3 entirely pale .... ***A. andywarreni* n. sp.** females



Couplet 44

45(43)A. Metapleuron and propodeum both entirely black .... ***A. bobpoolei* n. sp.** females

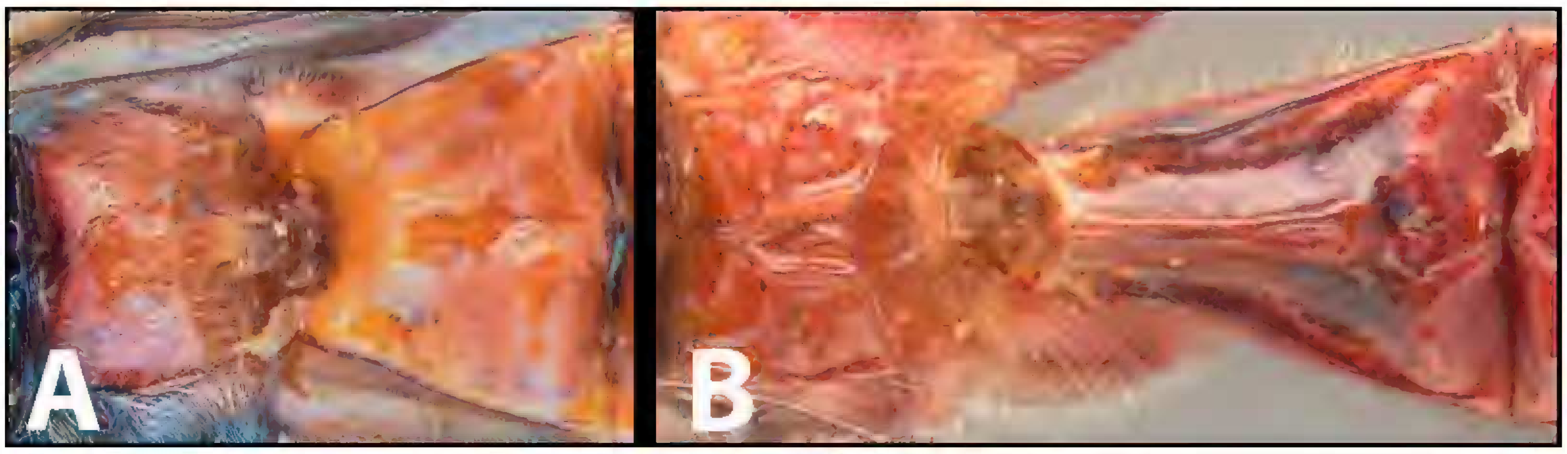
45(43)B. Metapleuron and propodeum from mostly black to entirely yellow, one or the other always with some yellow/orange color .... *A. janzeni* males



Couplet 45

46(42)A. First tergum varying from weakly convex to with a rounded longitudinal bulge 47

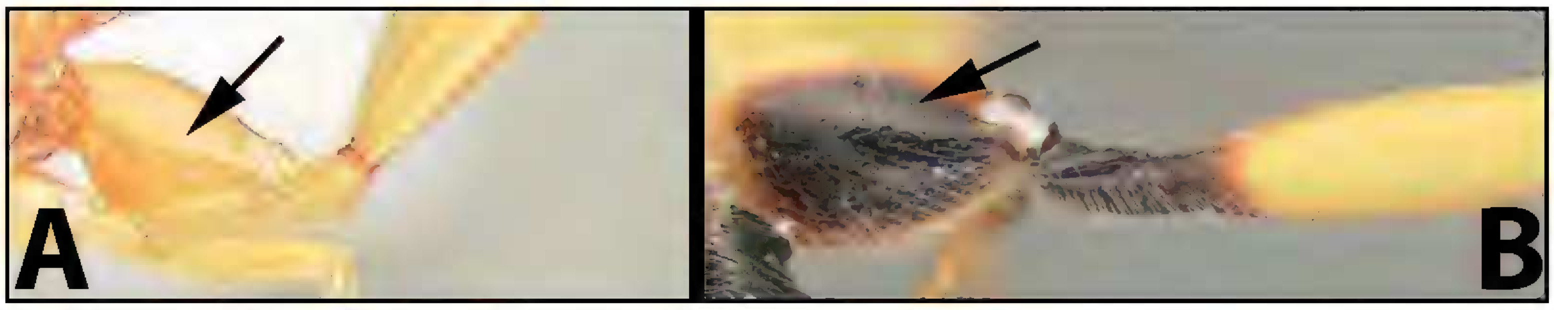
46(42)B. First tergum with well-defined median longitudinal carina 49



Couplet 46

47(46)A. Hind coxa entirely pale 48

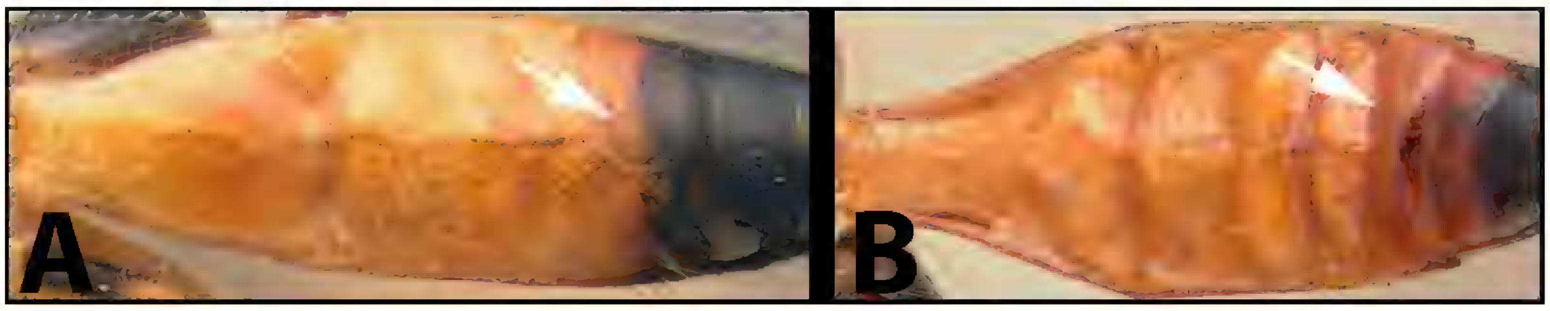
47(46)B. Hind coxa mostly pale with a melanic patch laterally or a vertical melanic stripe .... ***A. almasolisae* n. sp.** females



Couplet 47

48(47)A. Third tergum lacking transverse depression or depression barely indicated; metapleuron entirely pale ....***A. iankitchingi* n. sp.**

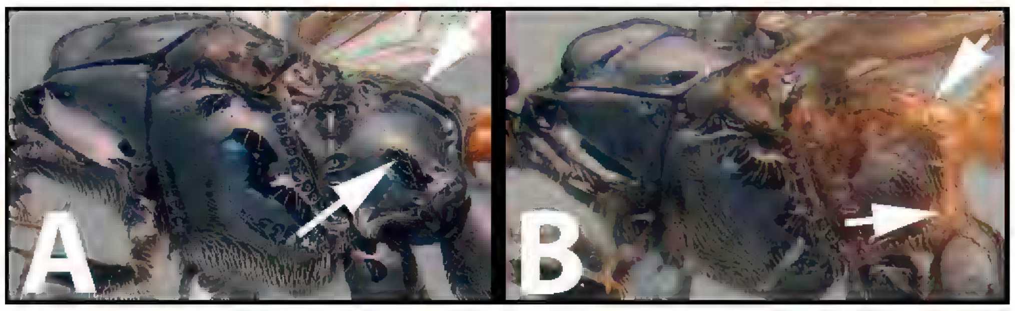
48(47)B. Third tergum with deep transverse depression; metapleuron partly or entirely melanic......................................***A. tommyersi* n. sp.**



Couplet 48

49(46)A. Metapleuron and propodeum both entirely black ....***A. bobpoolei* n. sp.** females

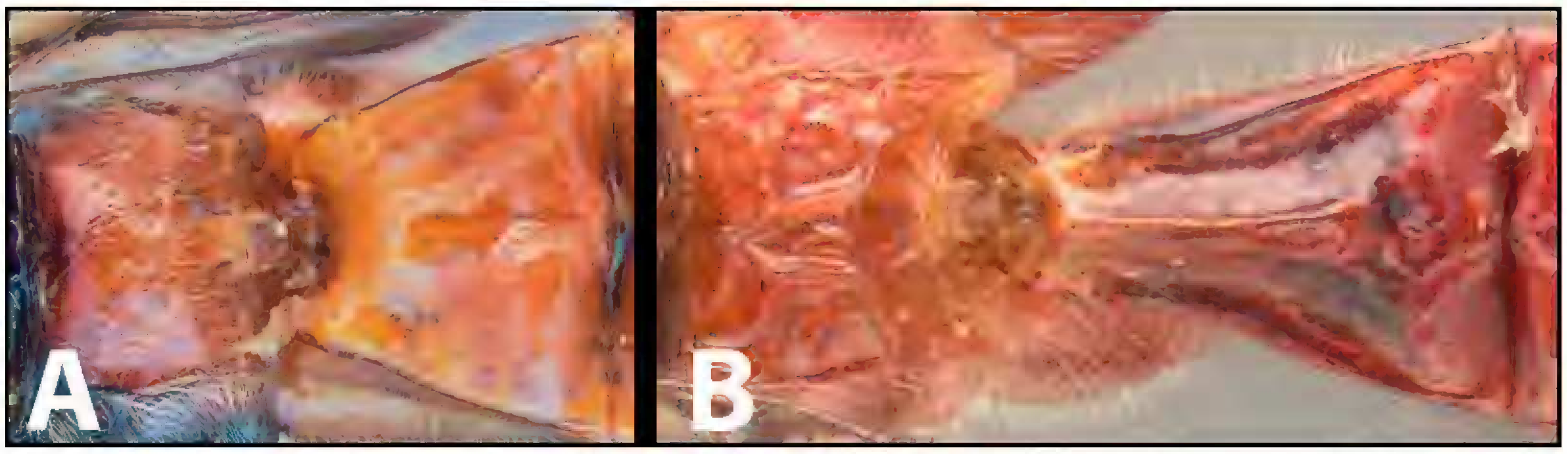
49(46)B. Metapleuron and propodeum from mostly black to entirely yellow, one or the other always with some yellow color ....*A. janzeni* males



Couplet 49

50(42)A. First tergum varying from weakly convex to with a rounded longitudinal bulge 51

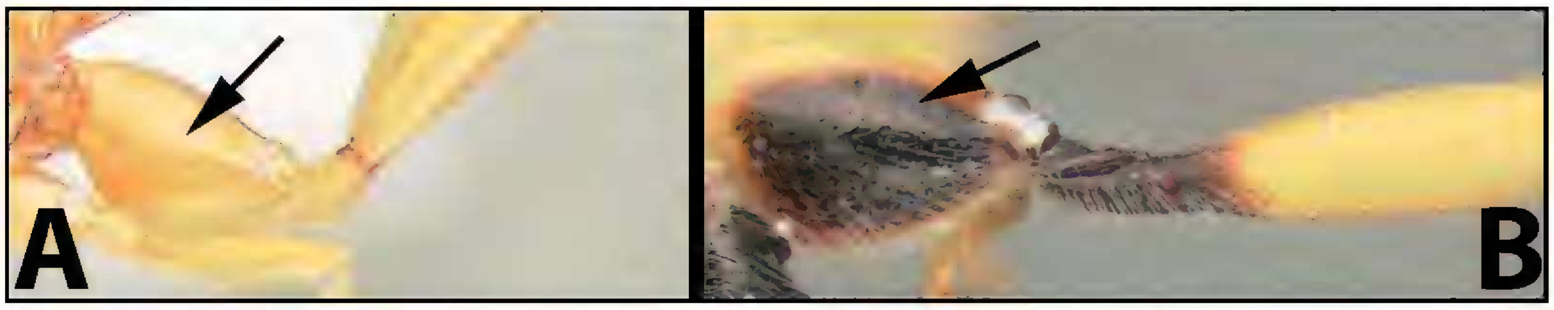
50(42)B. First tergum with well-defined median longitudinal carina 53



Couplet 50

51(50)A. Hind coxa entirely pale...52

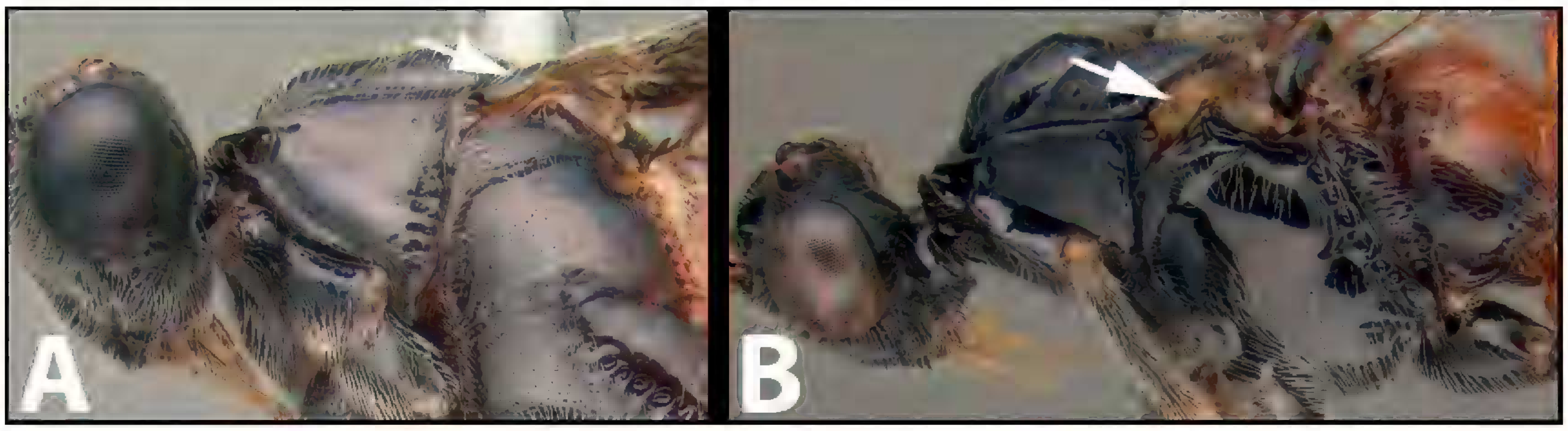
51(50)B. Hind coxa mostly pale with a vertical melanic stripe ....***A. marcepsteini* n. sp.**



Couplet 51

52(51)A. Tegula black .... ***A. malcolmscoblei* n. sp.**

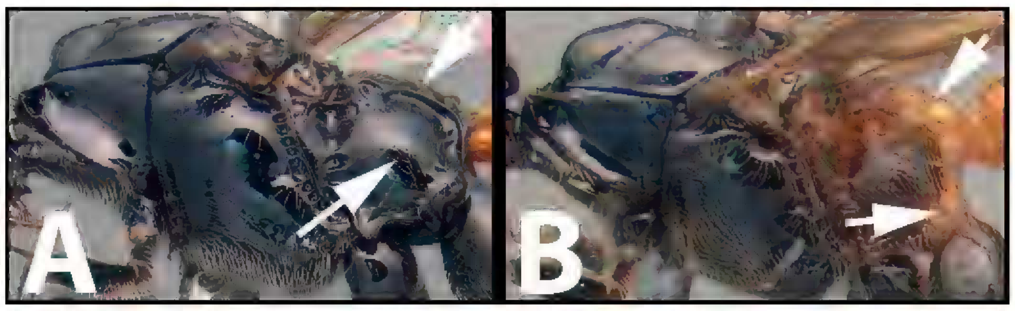
52(51)B. Tegula pale, yellow to orange .... ***A. nickgrishini* n. sp.**



Couplet 52

53(50)A. Metapleuron and propodeum both entirely black .... ***A. bobpoolei* n. sp.** females

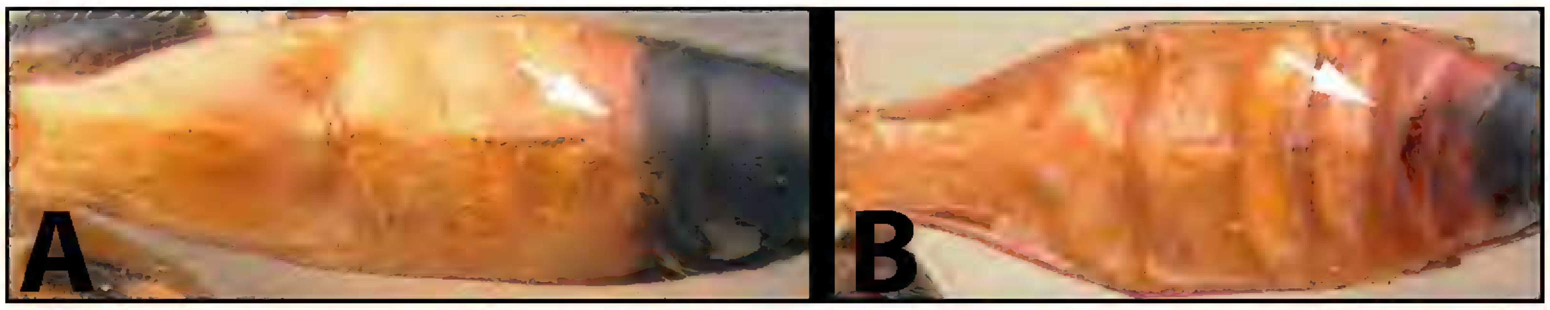
53(50)B. Metapleuron and propodeum from mostly black to entirely yellow, one or the other always with some yellow color .... *A. janzeni* males



Couplet 53

54(42)A. Third tergum lacking transverse depression or depression barely indicated 55

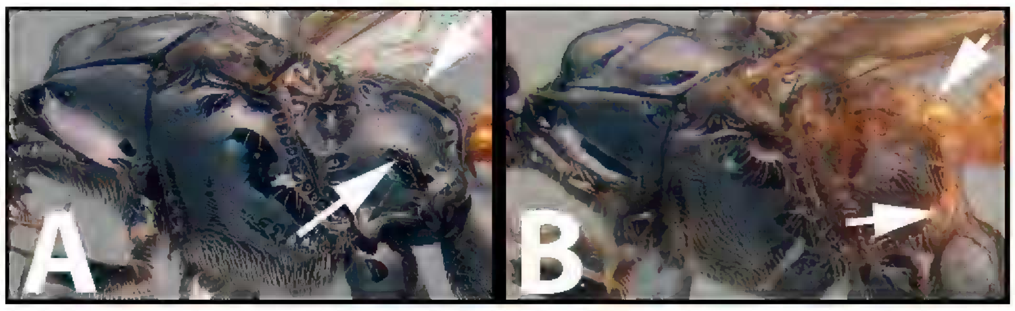
54(42)B. Third tergum with deep transverse depression 56



Couplet 54

55(54)A. Metapleuron mostly or entirely melanic; propodeum melanic .... ***A. bobpoolei* n. sp.** females

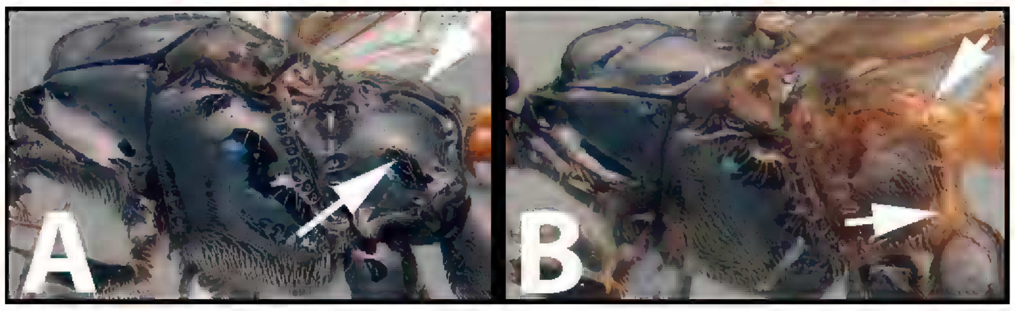
55(54)B. Metapleuron mostly or entirely pale; propodeum pale .... ***A. genemonroei* n. sp.**



Couplet 55

56(54)A. Metapleuron and propodeum both entirely black ....***A. bobpoolei* n. sp.** females

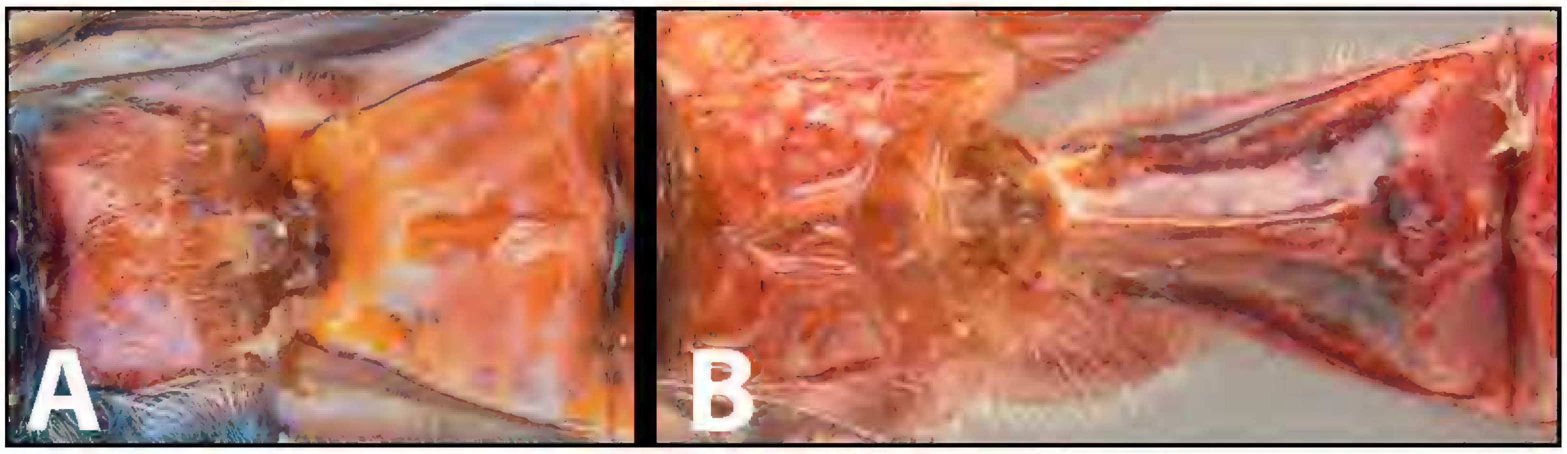
56(54)B. Metapleuron and propodeum from mostly black to entirely yellow, one or the other always with some yellow color ....*A. janzeni* males



Couplet 56

57(41)A. First tergum varying from weakly convex to with a rounded longitudinal bulge 58

57(41)B. First tergum with well-defined median longitudinal carina ....*A. janzeni*

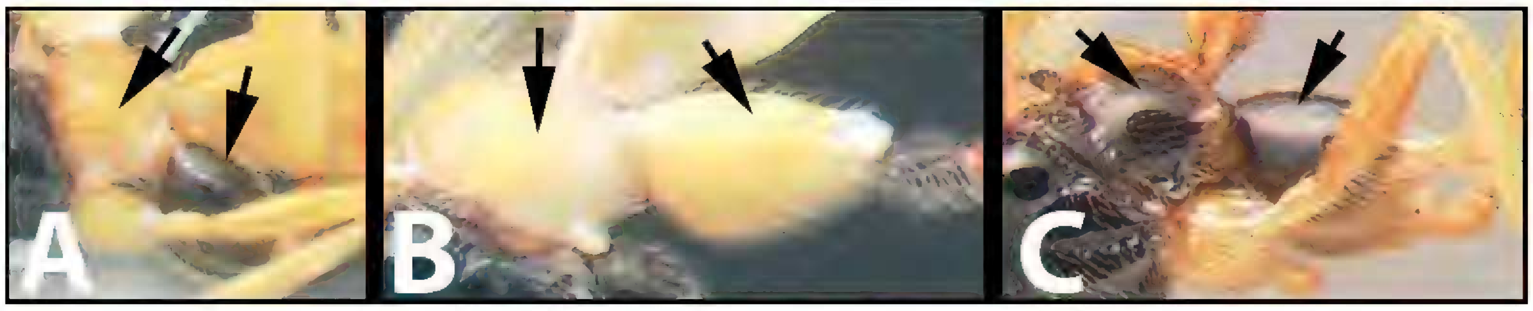


Couplet 57

58(57)A. Metapleuron mostly or entirely pale; hind coxa partly or entirely melanic ....***A. longinoi* n. sp.**

58(57)B. Metapleuron mostly or entirely pale; hind coxa entirely pale 59

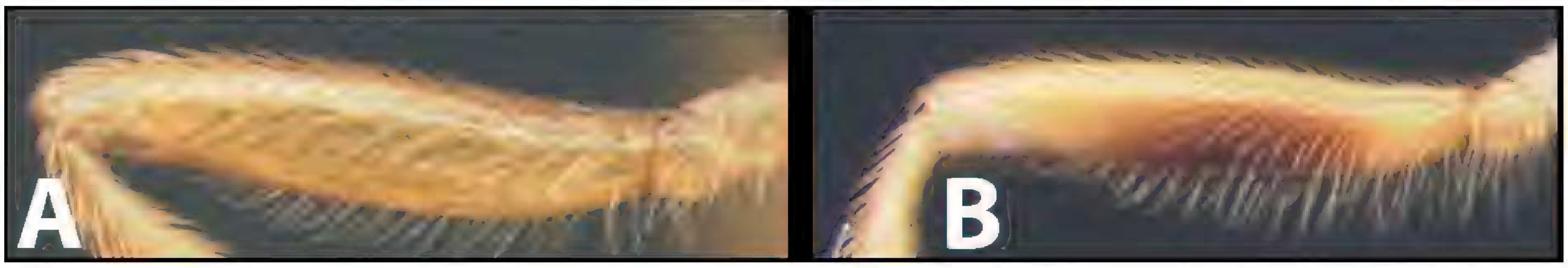
58(57)C. Metapleuron mostly or entirely melanic; hind coxa partly or entirely melanic ....***A. jeanmariecadioui* n. sp.**



Couplet 58

59(58)A. Femur of midleg entirely yellow 60

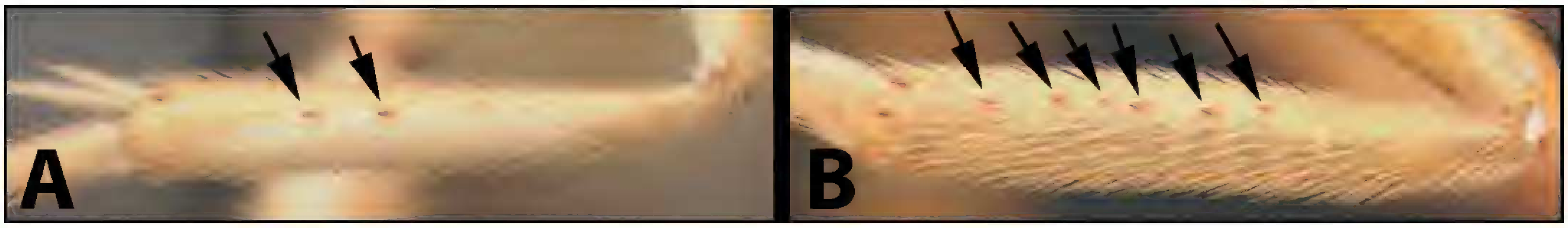
59(58)B. Femur of midleg mostly yellow but melanic at midlength, sometimes only ventrally....................................***A. fernandodiasi* n. sp.**



Couplet 59

60(59)A. Midtibia with 0–3 nonapical spines, precoxal sulcus shorter with fewer crenulae .... ***A. fernandezi* n. sp.**

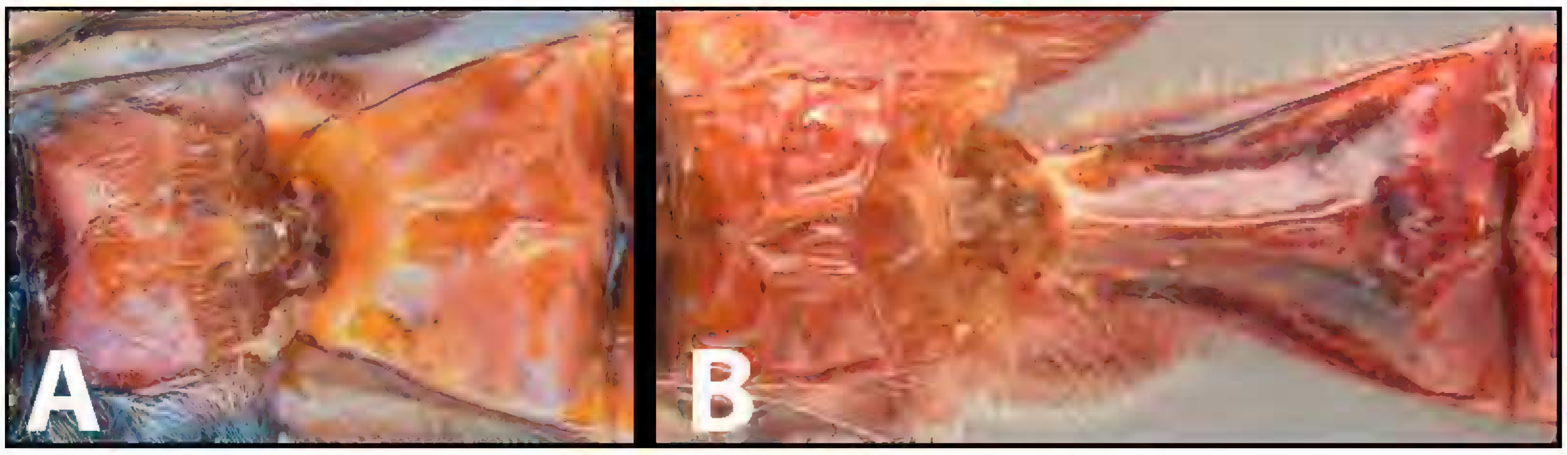
60(59)B. Midtibia with 5 or more nonapical spines; precoxal sulcus longer with more crenulae .... ***A. andresfreitasi* n. sp.**



Couplet 60

61(41)A. First tergum varying from weakly convex to with a rounded longitudinal bulge 62

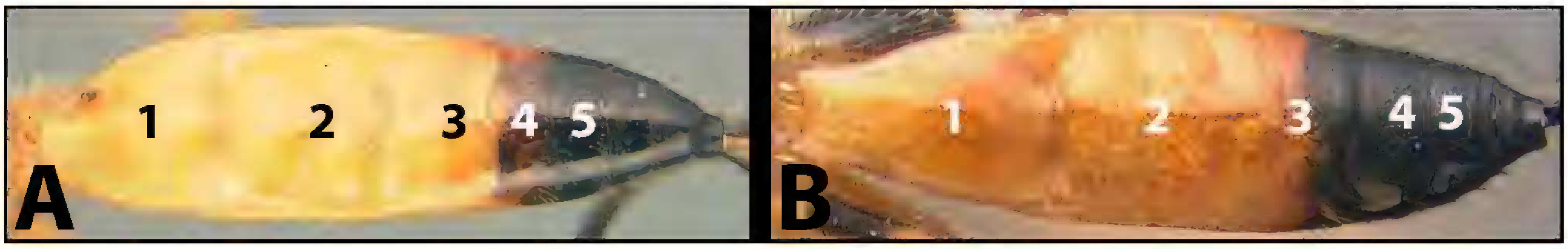
61(41)B. First tergum with well-defined median longitudinal carina .... *A. janzeni* males



Couplet 61

62(61)A. Median tergite 3 pale .... ***A. scottshawi* n. sp.**

62(61)B. Median tergite 3 pale anteriorly, melanic posteriorly.. ***A. jackiemillerae* n. sp.**

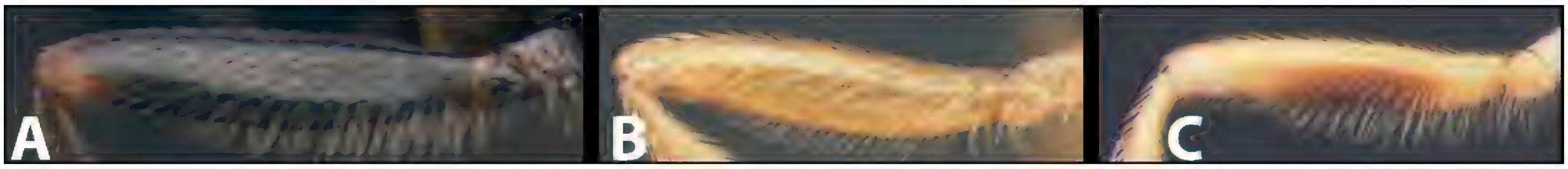


Couplet 62

63(2)A. Midfemur melanic...64

63(2)B. Midfemur pale..71

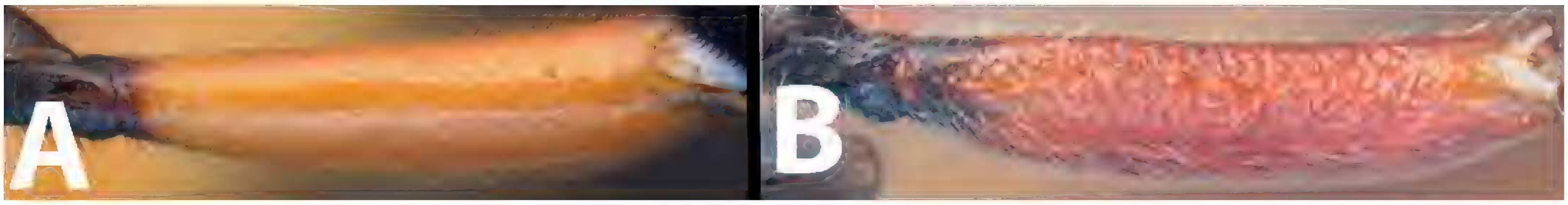
63(2)C. Midfemur bicolored, melanic and pale..77



Couplet 63

64(63)A. Hind femur with weak sparse punctures ventrally, little or no more heavily sculptured than dorsal surface....................................65

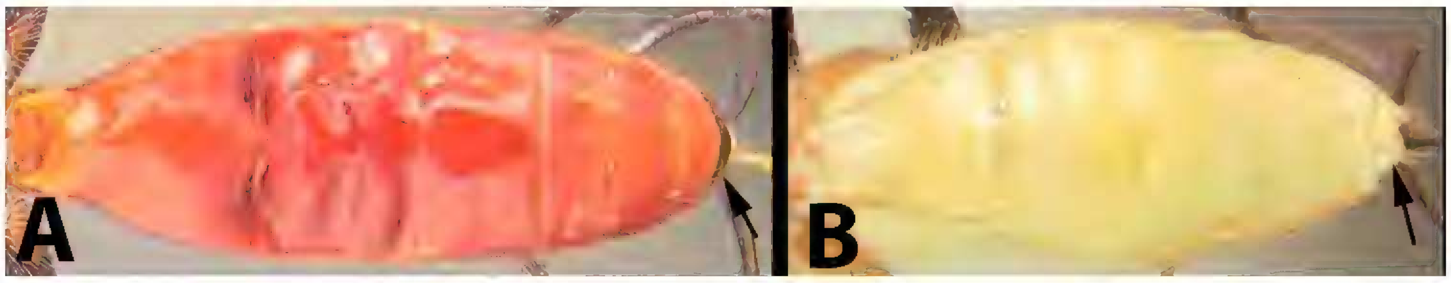
64(63)B. Hind femur heavily sculptured ventrally with aciculations or rugosities, distinctly more heavily sculptured than dorsal surface 69



Couplet 64

65(64)A. Penultimate metasomal tergum (and often more terga) melanic 66

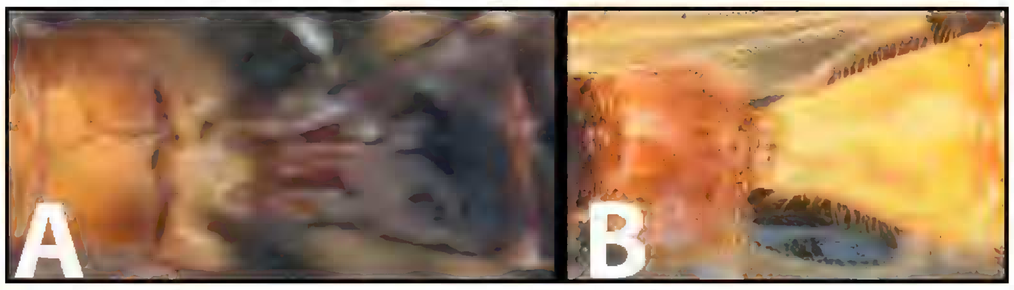
65(64)B. Penultimate metasomal tergum pale, reddish orange to yellow 67



Couplet 65

66(65)A. Propodeum areolate, with at least one closed areola; first tergum with well-defined median longitudinal carina............*A. cuna* male

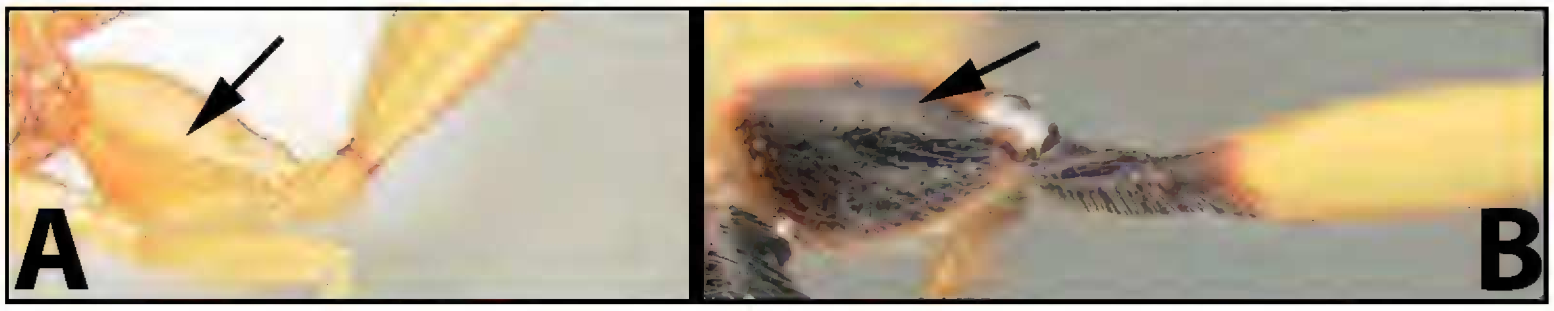
66(65)B. Propodeum lacking complete areolae, smooth; first tergum weakly convex to with a rounded longitudinal bulge ....*A. varius*



Couplet 66

67(65)A. Hind coxa entirely pale...***A. yuanmaofangi* n. sp.**

67(65)B. Hind coxa with a black patch laterally (may only be present near apex) 68



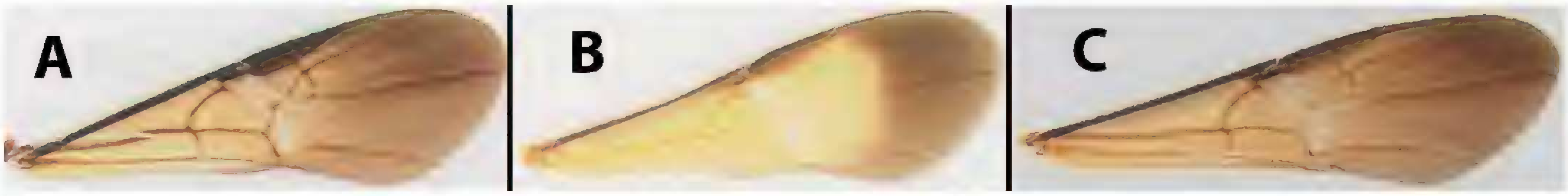
Couplet 67

68(67) These three species are very difficult to separate and this couplet has limited accuracy.

68(67)A. Forewing distinctly yellow in basal ⅔ but lacking a distinct margin between pale and dark areas. .... ***A. johnbrowni* n. sp.**

68(67)B. Forewing distinctly yellow in basal ⅔ and with a distinct margin between pale and dark areas .... *A. cocto*

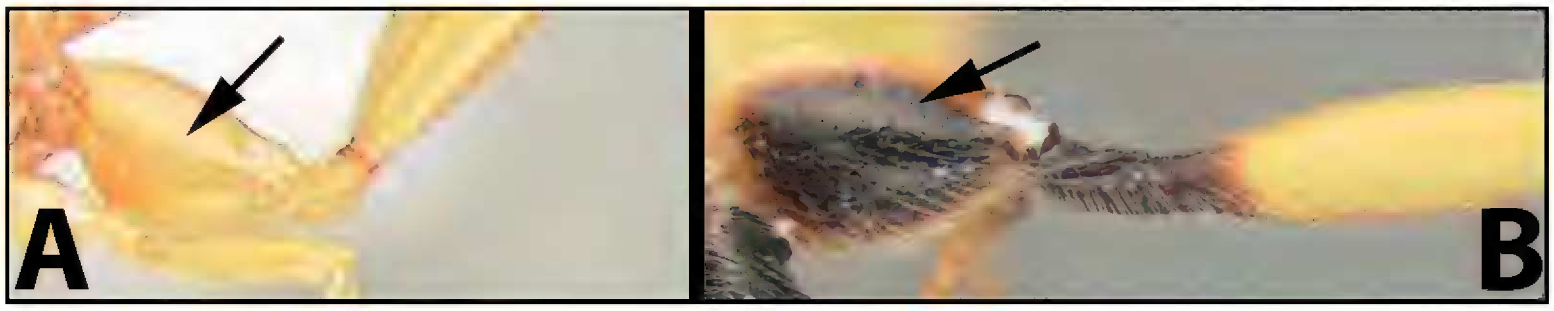
68(67)C. Forewing with only a hint of yellow basally .... ***A. mariaheikkilae* n. sp.**



Couplet 68

69(64)A. Hind coxa entirely pale .... *A. arawak*

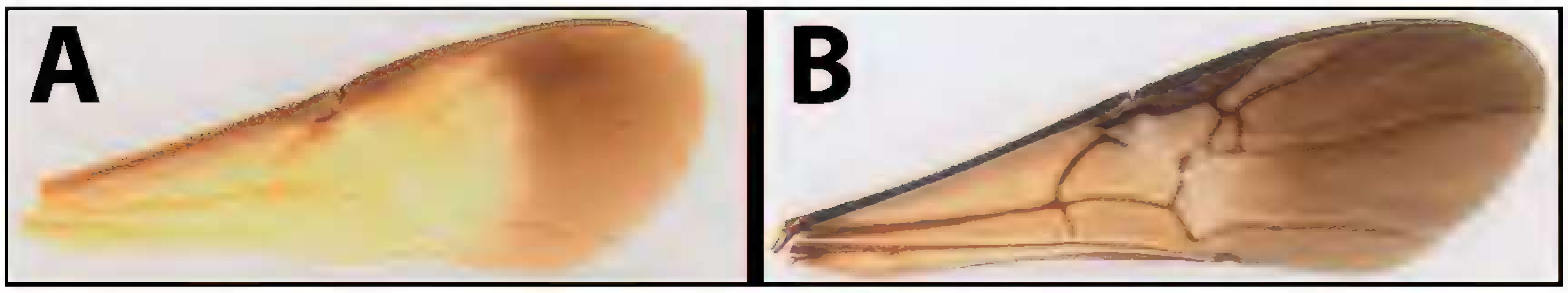
69(64)B. Hind coxa with a black patch laterally (may only be present near apex) 70



Couplet 69

70(69)A. Forewing with a well-defined margin between apical infuscate area and basal yellow area .... ***A. brendameierottoae* n. sp.**

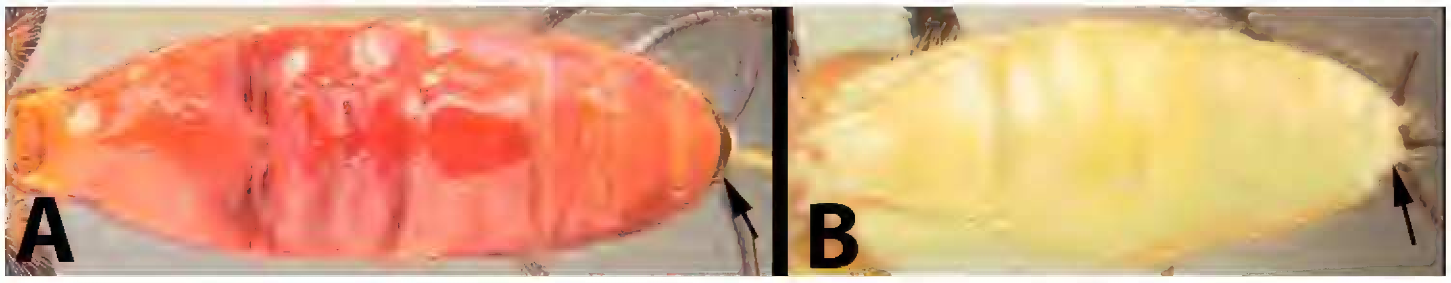
70(69)B. Forewing lacking a well-defined margin between apical infuscate area and basal pale area .... ***A. paulheberti* n. sp.**



Couplet 70

71(63)A. Penultimate metasomal tergum melanic 72

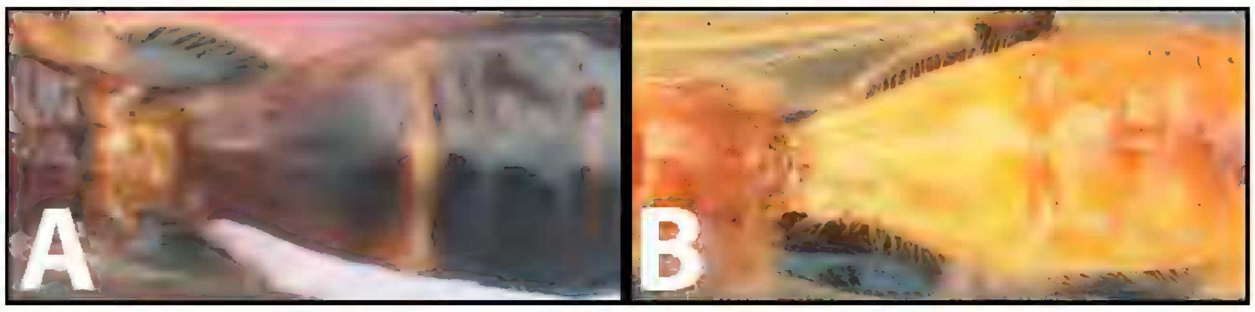
71(63)B. Penultimate metasomal tergum pale, reddish orange to yellow 74



Couplet 71

72(71)A. Median tergites 1 and 2 mostly or entirely melanic .... ***A. scottmilleri* n. sp.** male

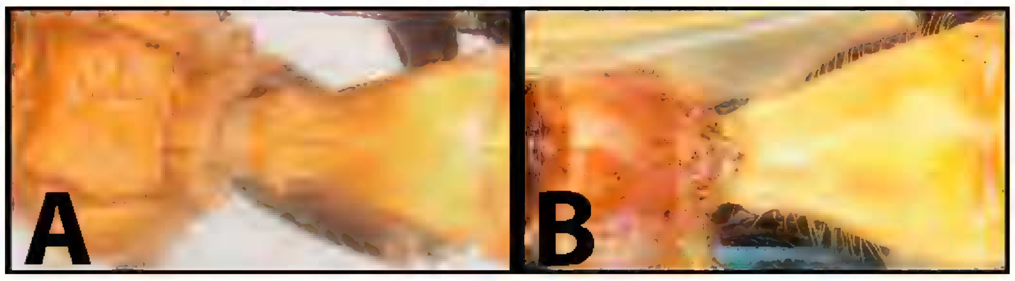
72(71)B. Median tergites 1 and 2 pale 73



Couplet 72

73(72)A. Propodeum areolate, with at least one closed areola .... ***A. kaydodgeae* n. sp.**

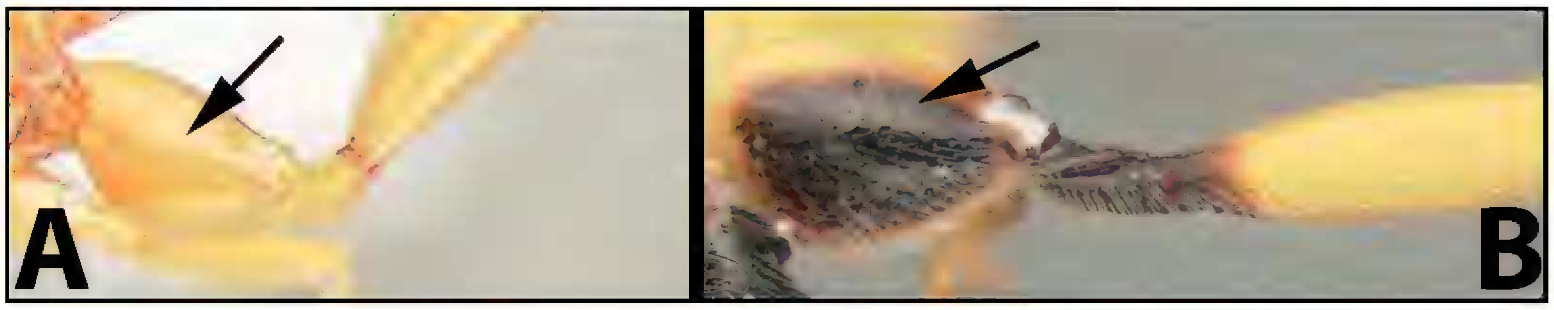
73(72)B. Propodeum lacking complete areolae, mostly or completely smooth .... *A. varius*



Couplet 73

74(71)A. Hind coxa entirely pale 75

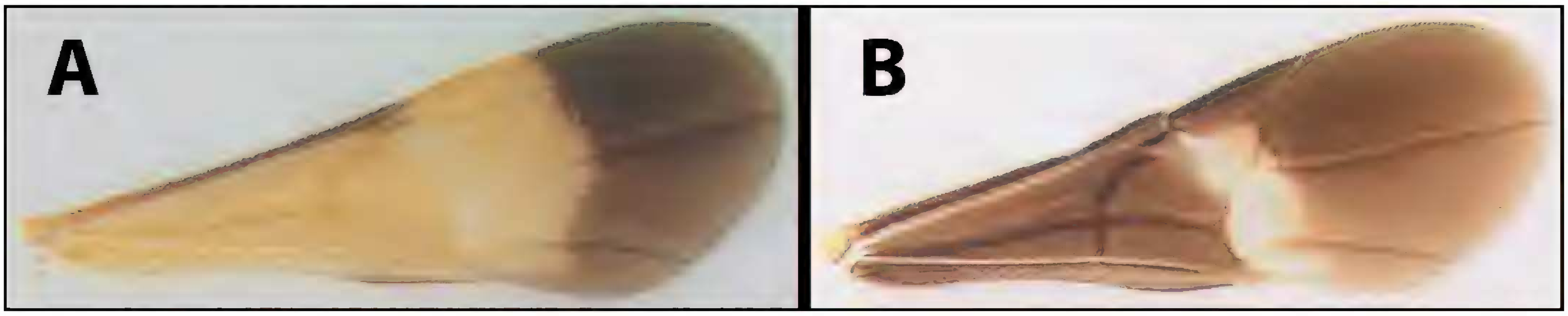
74(71)B. Hind coxa with a black patch laterally or near apex 76



Couplet 74

75(74)A. Forewing yellow in basal ⅔, melanic apically .... *A. cuna* female

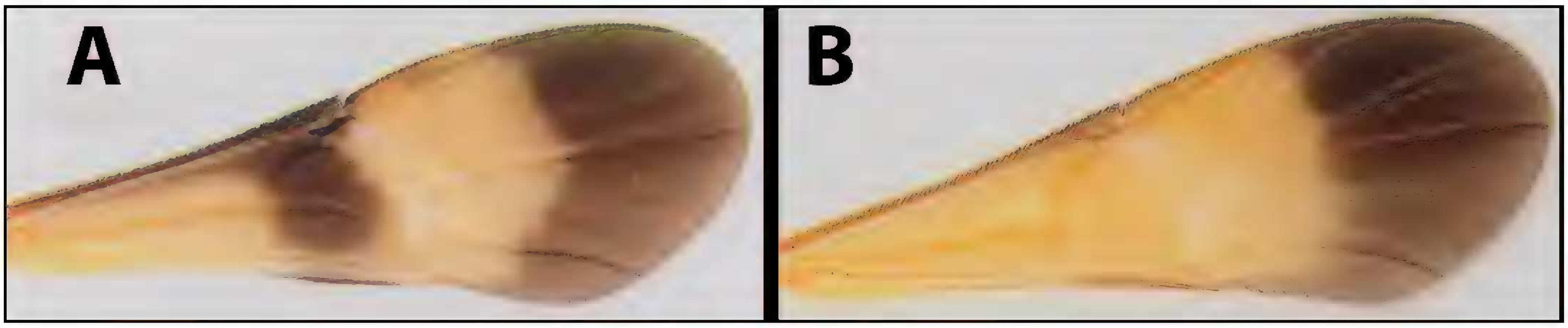
75(74)B. Forewing mostly melanic with a clear vertical band near stigma .... ***A. donlafontainei* female**



Couplet 75

76(73)A. Forewing banded from base: yellow, infuscate, yellow, infuscate............ ***A. scottmilleri* n. sp.** female

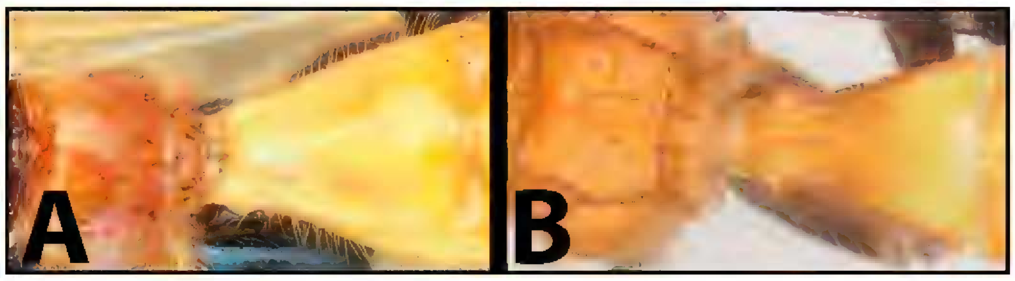
76(73)B. Forewing yellow basally, infuscate apically............ *A. cara*



Couplet 76

77(63)A. Propodeum lacking complete areolae, mostly or completely smooth............ *A. varius*

77(63)B. Propodeum areolate, with at least one closed areola............ ***A. donlafontainei* n. sp.** male



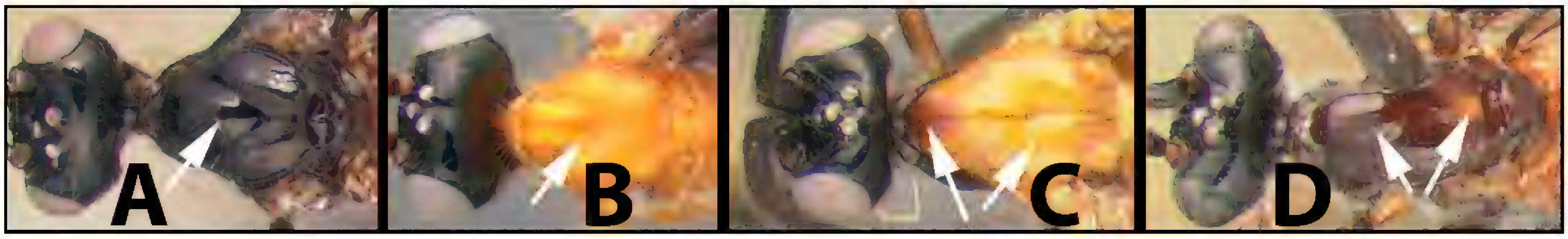
Couplet 77

78(1)A. Mesoscutum entirely melanic............79

78(1)B. Mesoscutum entirely pale............111

78(1)C. Mesoscutum mostly pale with some melanic infusions............142

78(1)D. Mesoscutum mostly melanic with some pale infusions............144

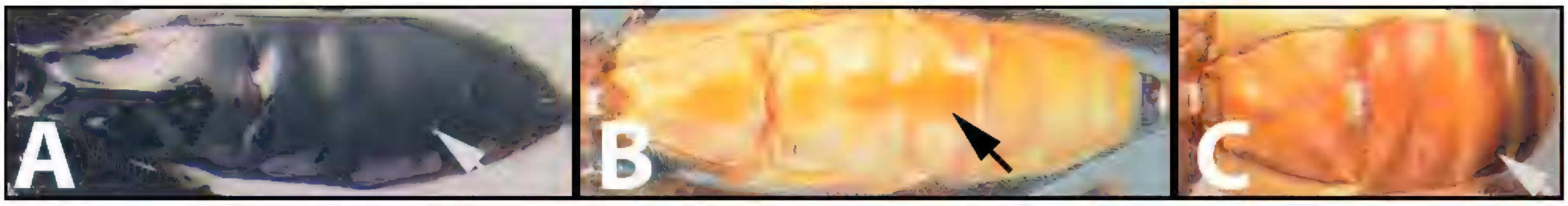


Couplet 78

79(78)A. Median tergite 3 melanic............80

79(78)B. Median tergite 3 pale............83

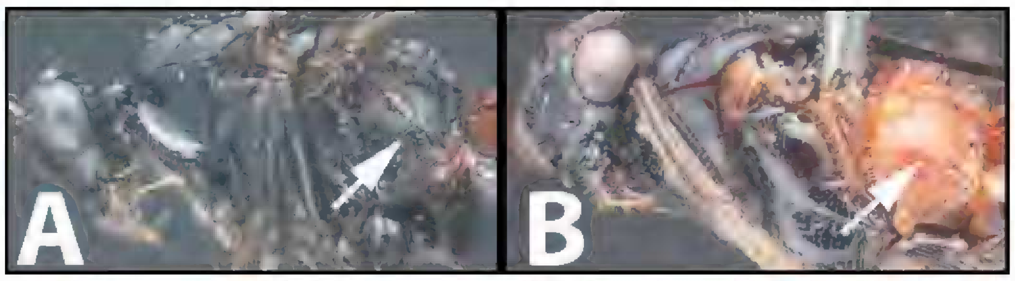
79(78)C. Median tergite 3 pale anteriorly, melanic posteriorly............ ***A. yuchinkengae* n. sp.**



Couplet 79

80(79)A. Metapleuron mostly or entirely melanic 81

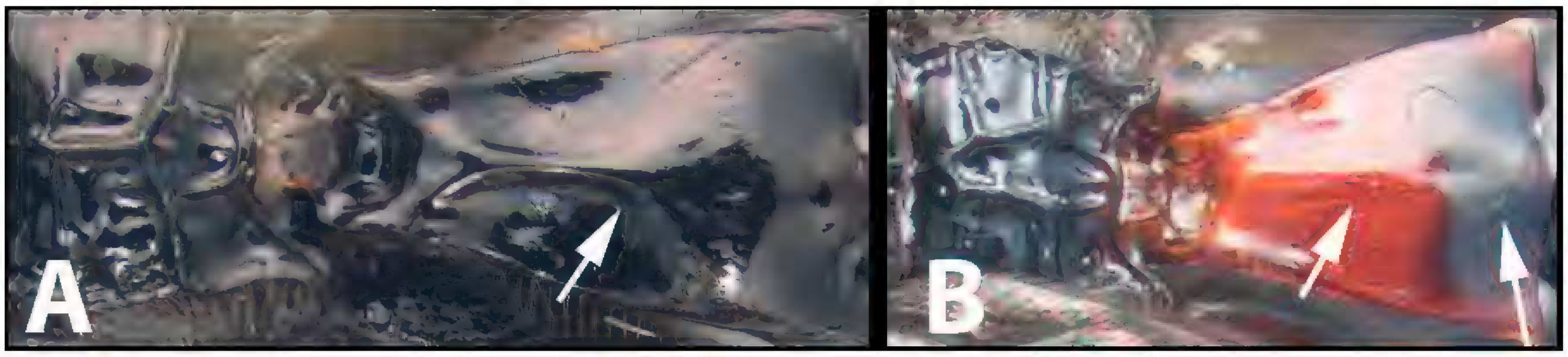
80(79)B. Metapleuron mostly or entirely pale ....***A. semihespenheidei* n. sp.**



Couplet 80

81(80)A. Median tergite 1 entirely melanic 82

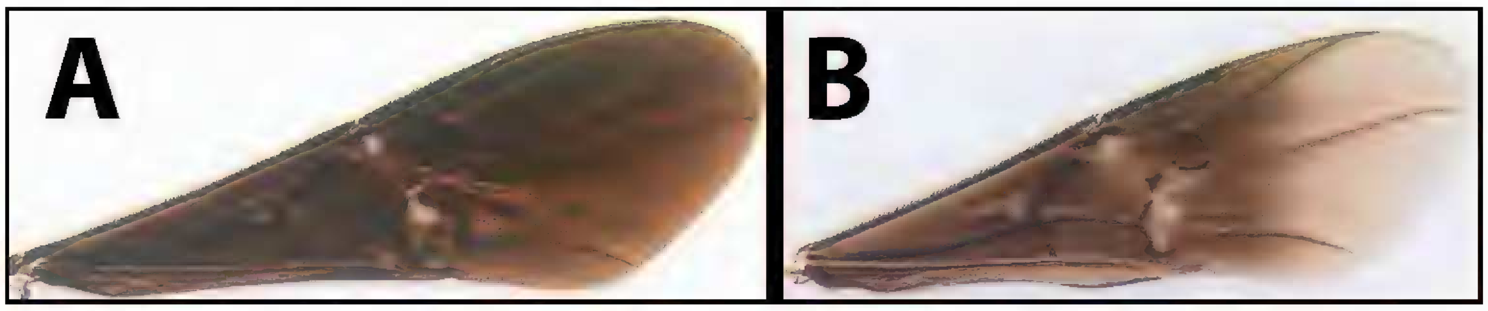
81(80)B. Median tergite 1 partly or completely pale (reddish) ....***A. hespenheidei* n. sp.**



Couplet 81

82(81)A. Forewing almost entirely infuscate, ignore small clear patches posteriad stigma ....*A. ekchuah*

82(81)B. Forewing patterned with a clear or white area apically ....***A. tanyadapkeyae* n. sp.**

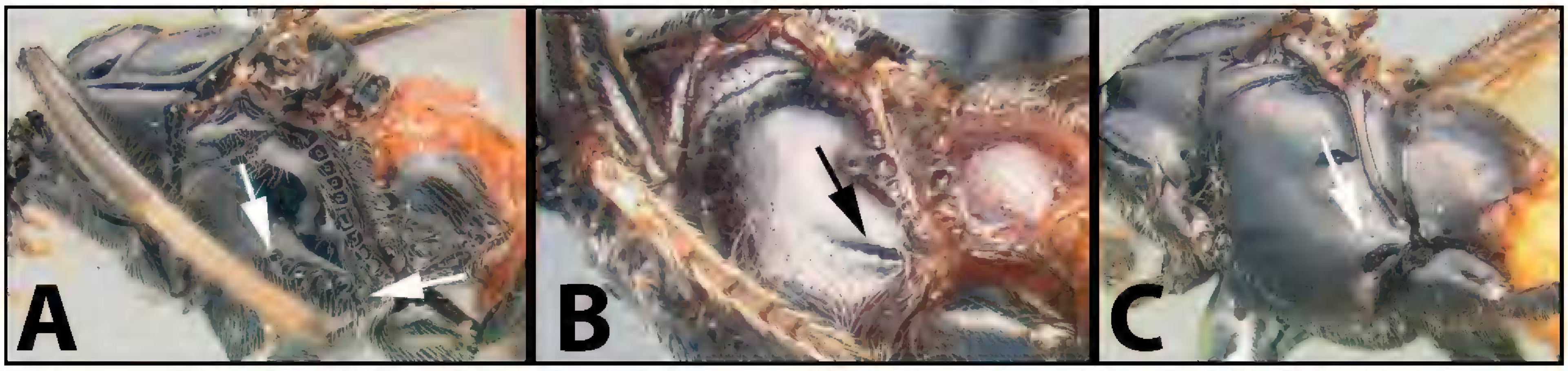


Couplet 82

83(79)A. Precoxal sulcus distinct and foveolate ½ or more length of mesopleuron 96

83(79)B. Precoxal sulcus with one or several distinct foveae posteroventrally, with or without a smooth groove extending anteriorly 84

83(79)C. Precoxal sulcus absent or mostly absent, represented at most by small, shallow depression, usually posteriorly, crenulae always lacking 105

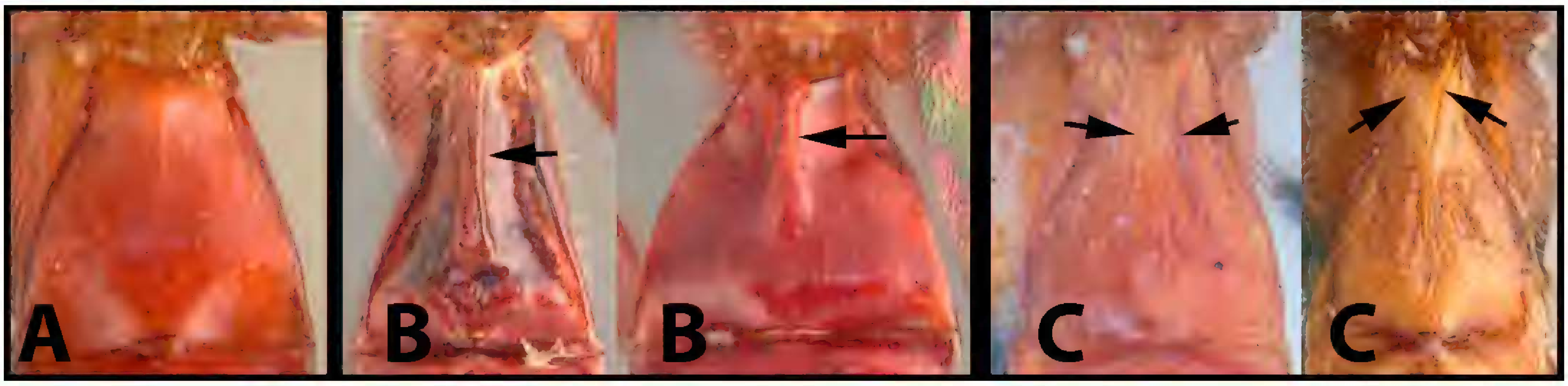


Couplet 83

84(83)A. First tergum varying from weakly convex to with a rounded longitudinal bulge 85

84(83)B. First tergum with well-defined median longitudinal carina 92

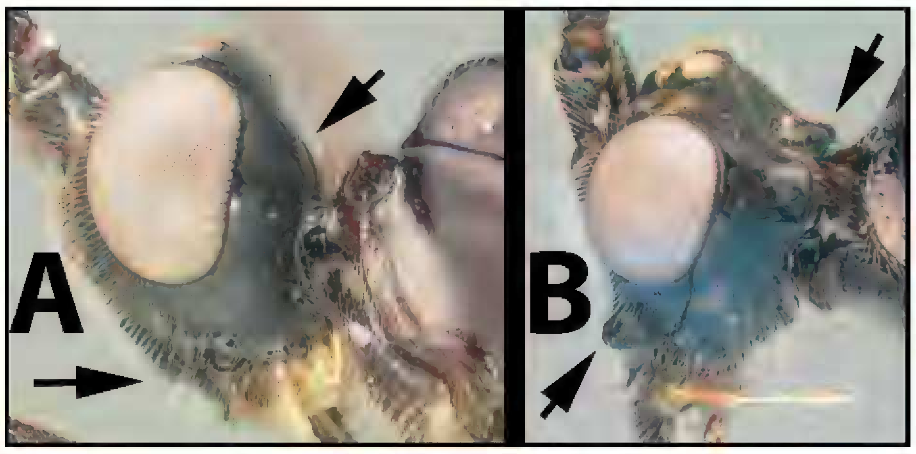
84(83)C. First tergum with two converging longitudinal carinae 95



Couplet 84

85(84)A. Occiput dorsolaterally rounded; clypeus unmodified, lacking protuberances........86

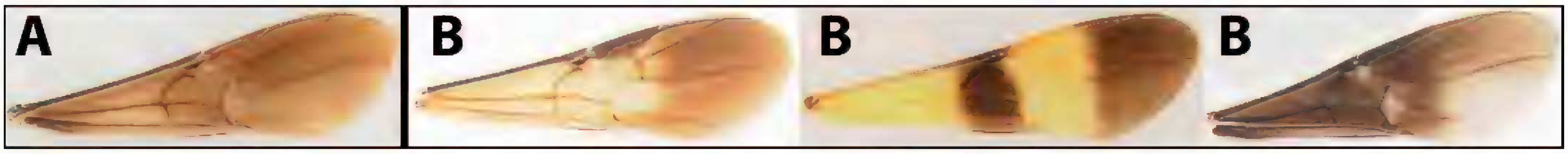
85(84)B. Occiput dorsolaterally with squared protuberances; clypeus with lateral protuberances .... ***A. victoriapookae* n. sp.**



Couplet 85

86(85)A. Forewing almost entirely infuscate, ignore small clear patches posteriad stigma 87

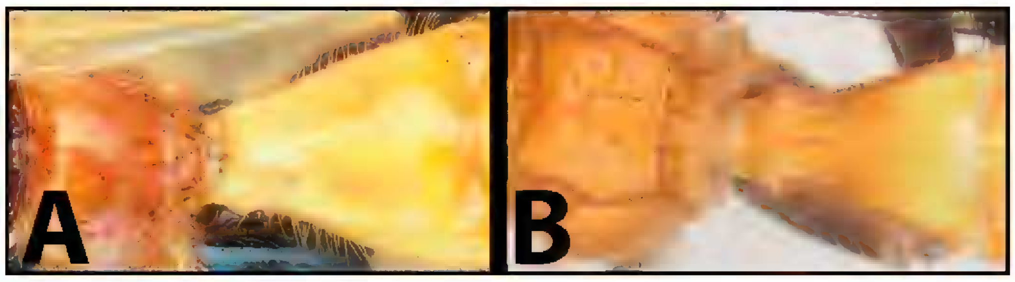
86(85)B. Forewing patterned with large clear, white, or yellow areas........90



Couplet 86

87(86)A. Propodeum smooth........89

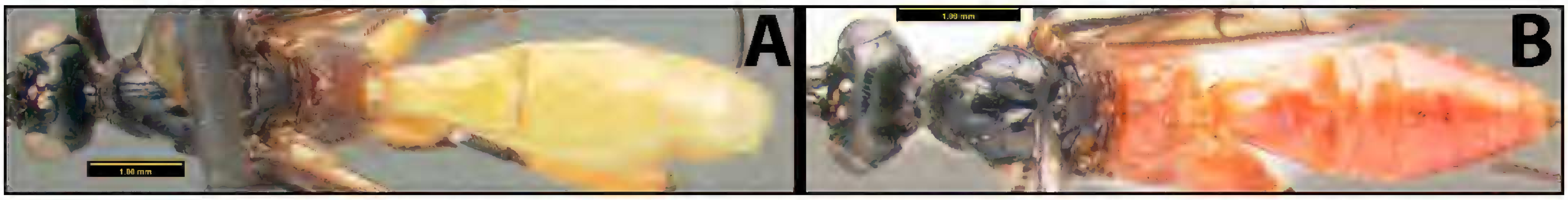
87(86)B. Propodeum sculptured 88



Couplet 87

88(87)A. Body color black and yellow .... ***A. johnburnsi* n. sp.**

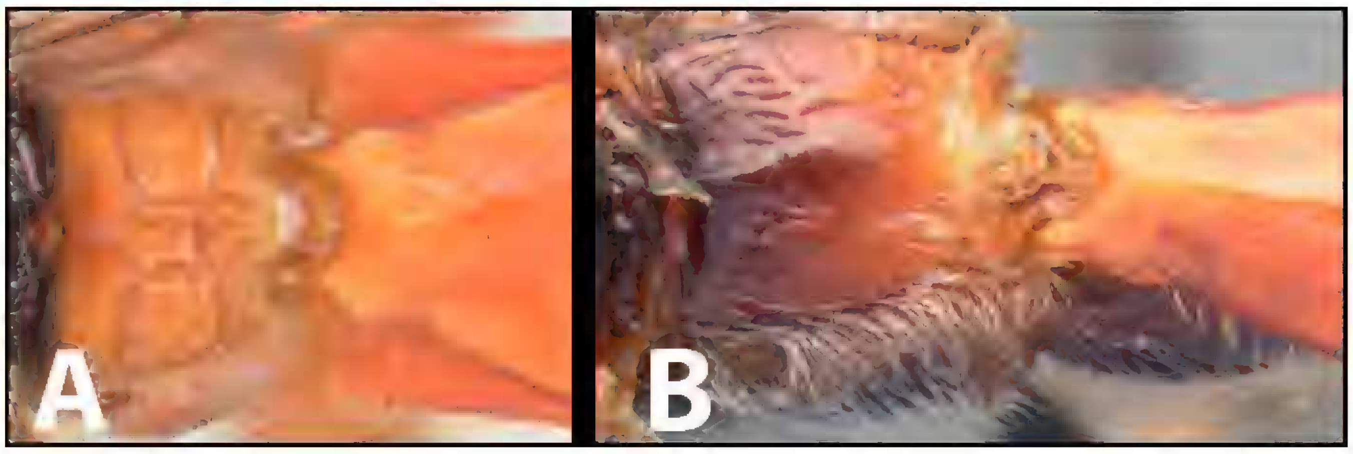
88(87)B. Body color black and orange to black and red .... ***A. markmetzi* n. sp.**



Couplet 88

89(87)A. Propodeum areolate, with several closed areolae .... ***A. markmetzi* n. sp.**

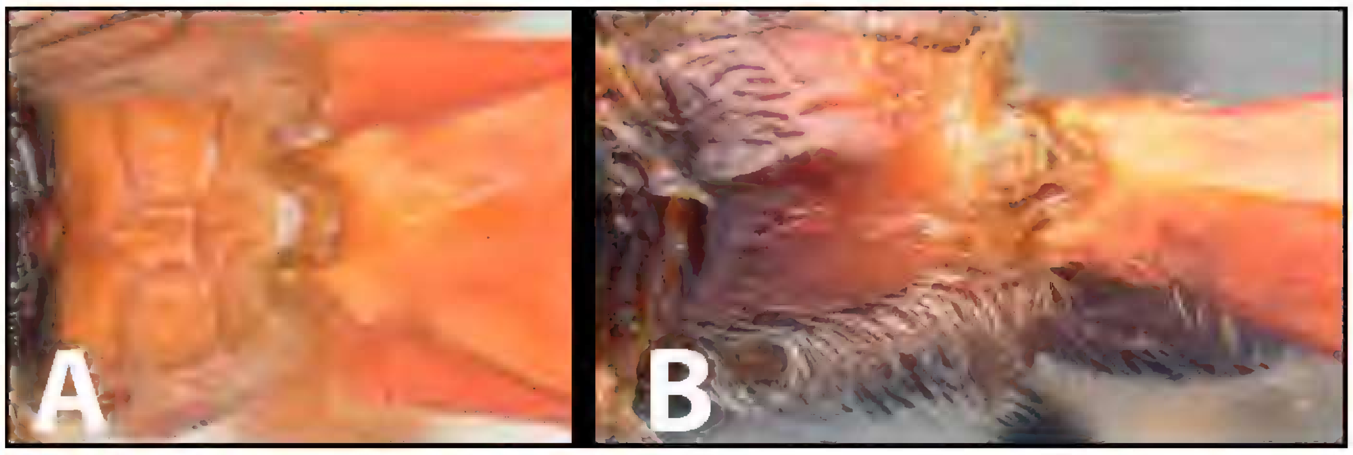
89(87)B. Propodeum lacking, complete areolae, mostly or completely smooth .... ***A. johnobryckii* n. sp.**



Couplet 89

90(86)A. Propodeum areolate, with at least one closed areola .... ***A. markmetzi* n. sp.**

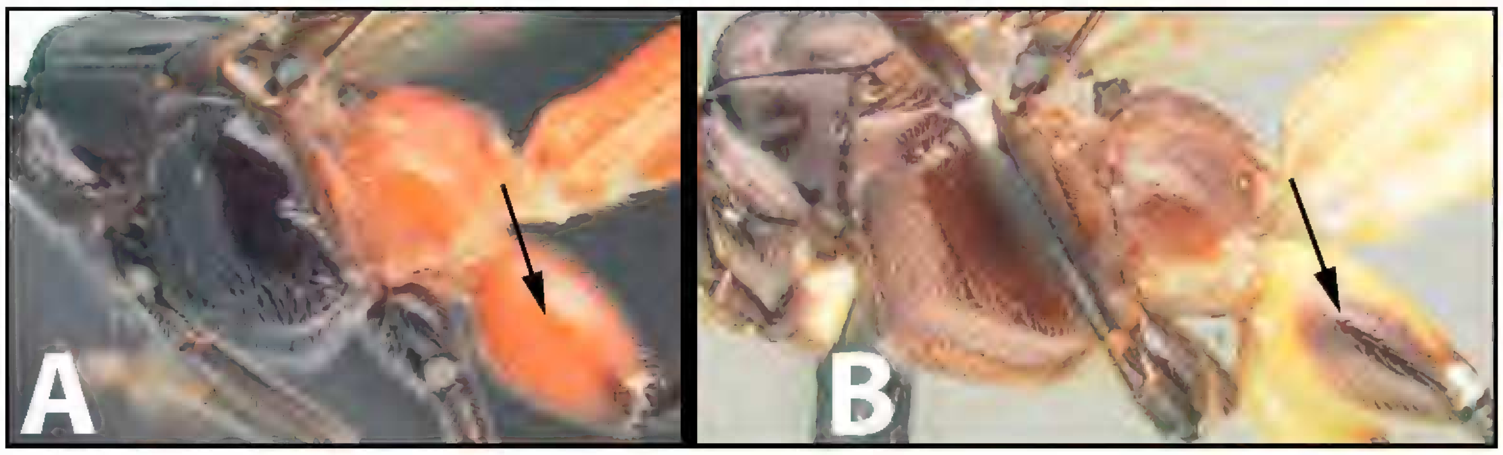
90(86)B. Propodeum lacking complete areolae, usually mostly or completely smooth 91



Couplet 90

91(90)A. Hind coxa entirely or almost entirely pale; hind femur mostly or entirely melanic .... *A. englishi*

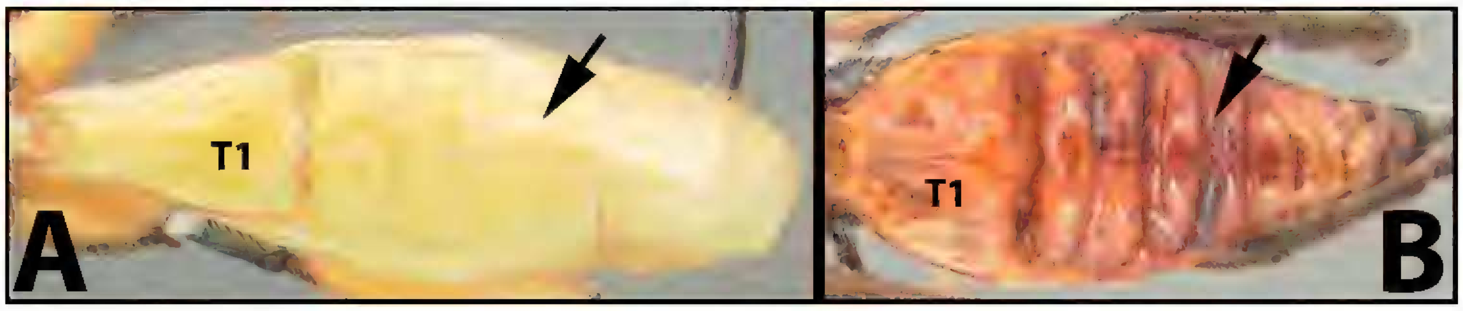
91(90)B. Hind coxa pale with a large melanic patch laterally; hind femur mostly or entirely pale .... ***A. johnburnsi* n. sp.**



Couplet 91

92(84)A. First median tergite longer than wide; third tergum lacking transverse depression or depression barely indicated 93

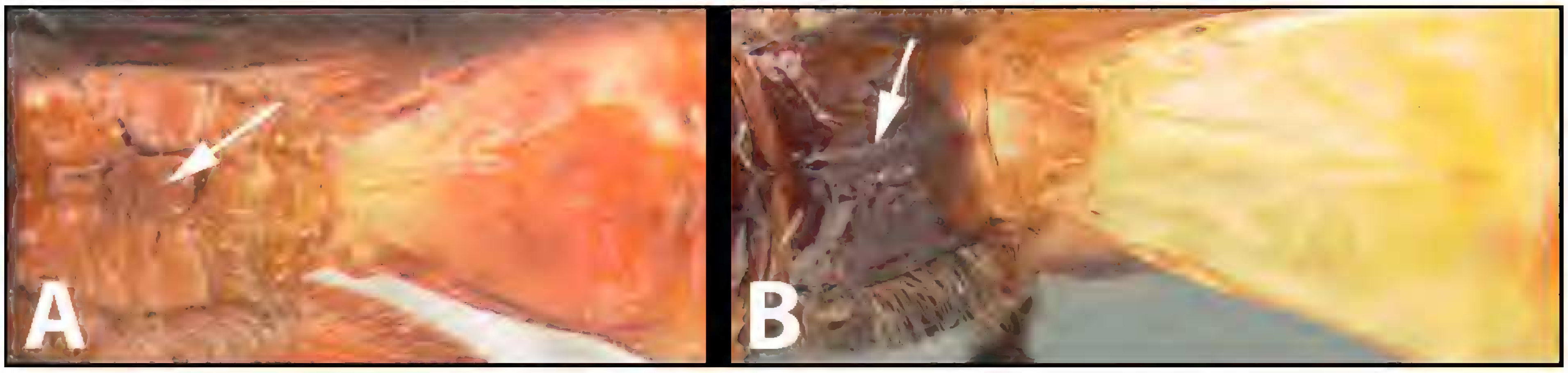
92(84)B. First median tergite wider than long; third tergum with deep transverse depression .... *A. miqa*



Couplet 92

93(92)A. Propodeum with more defined and complete sculpture; first median tergite mostly orange 94

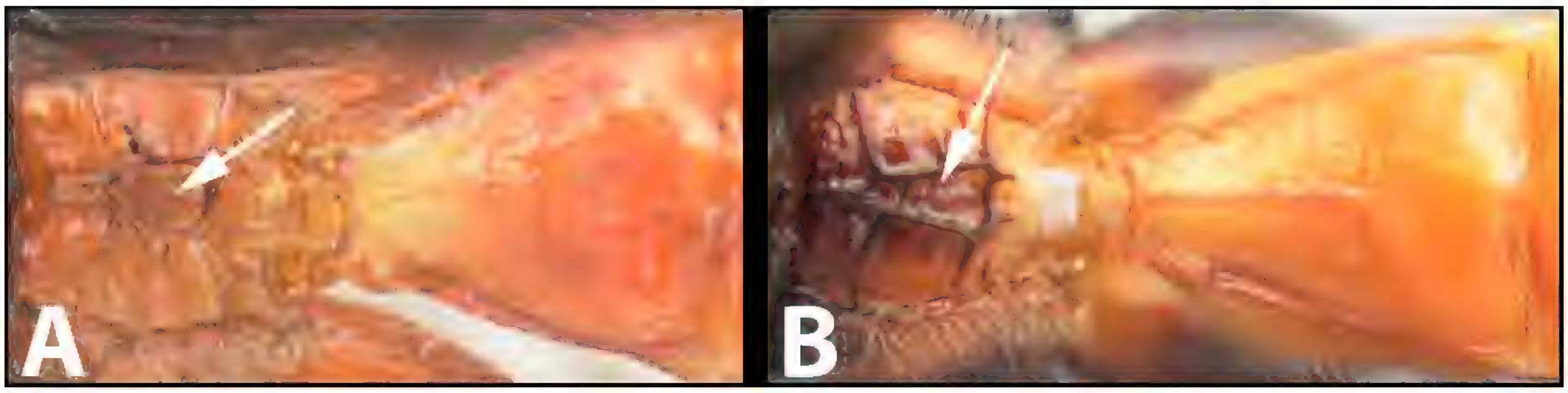
93(92)B. Propodeum with less defined and complete sculpture; first median tergite yellow .... ***A. johnburnsi* n. sp.**



Couplet 93

94(93)A. Propodeum and metapleuron entirely pale .... ***A. sarahmeierottoae* n. sp.** male

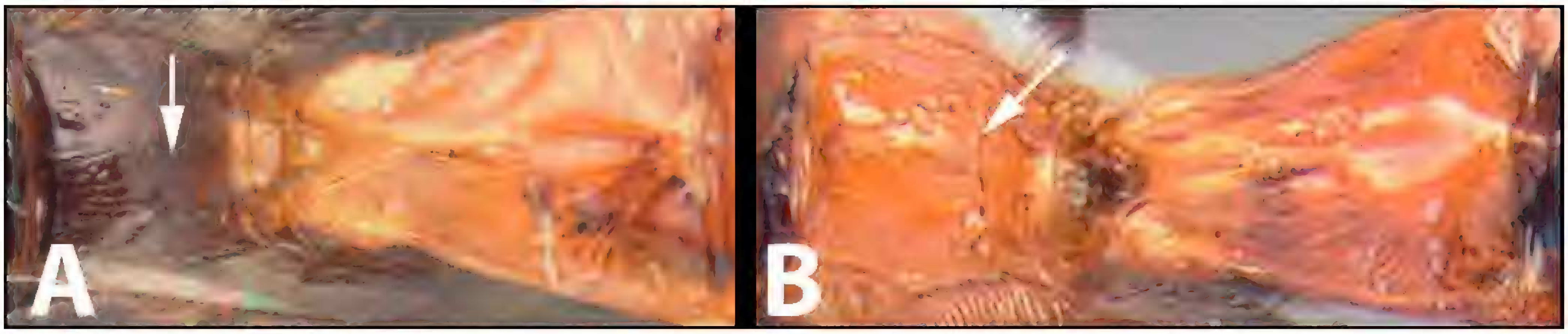
94(93)B. Propodeum and metapleuron with melanic color .... ***A. johnobryckii* n. sp.**



Couplet 94

95(84)A. Propodeum smooth, melanic .... ***A. barbsharanowskiae* n. sp.** female

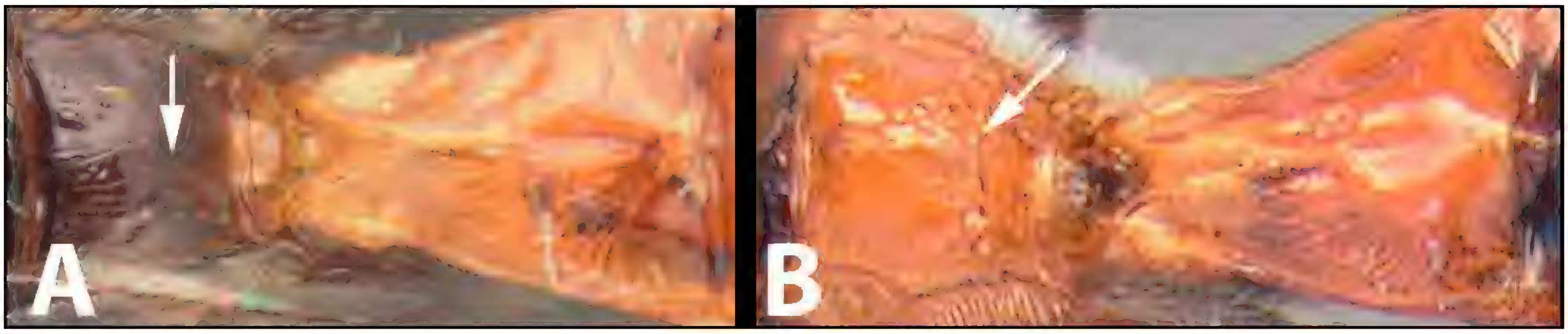
95(84)B. Propodeum sculptured, pale .... ***A. kaciejoae* n. sp.**



Couplet 95

96(83)A. Propodeum melanic 97

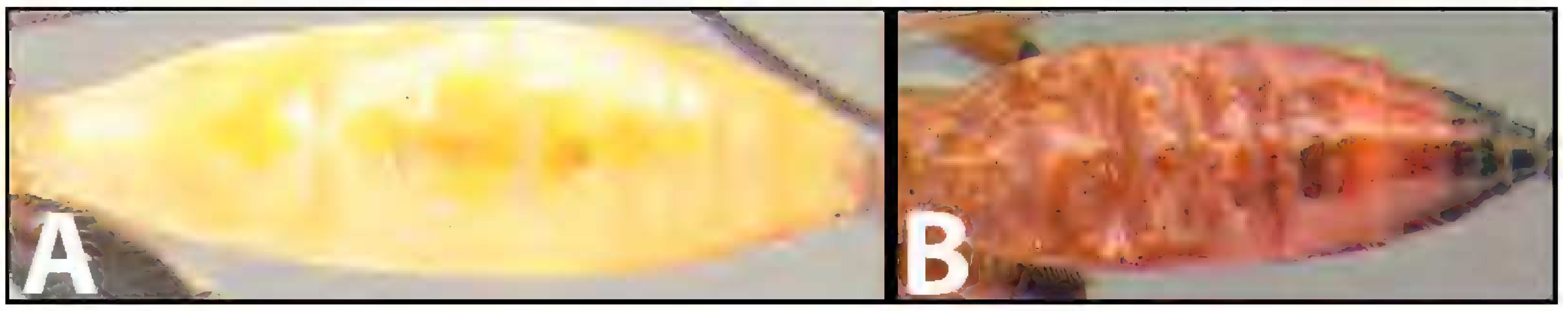
96(83)B. Propodeum pale 99



Couplet 96

97(95)A. Metasoma mostly or entirely yellow .... ***A. keithwillmotti* n. sp.**

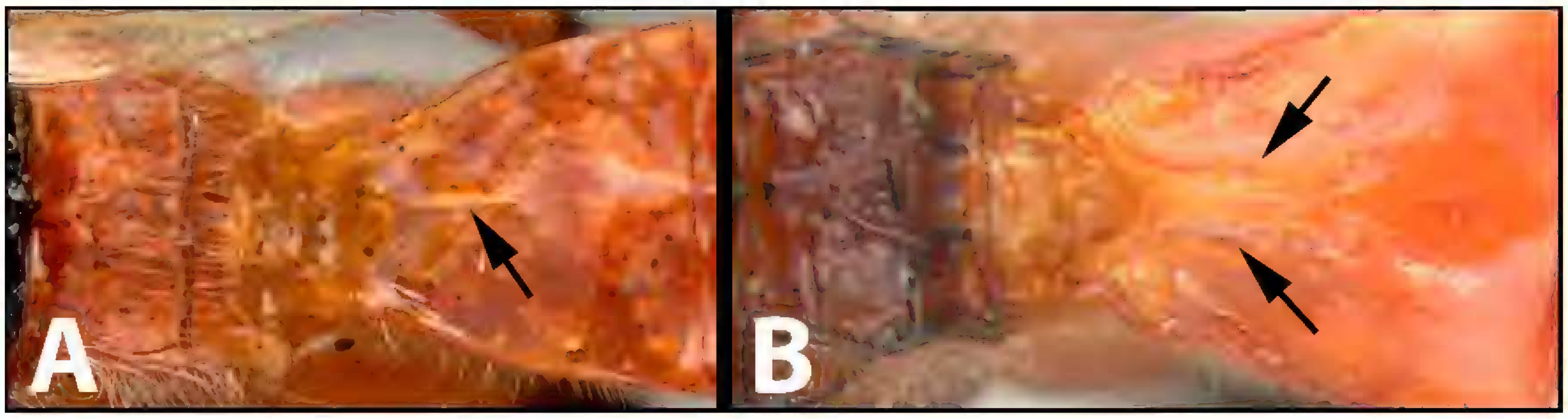
97(95)B. Metasoma mostly or entirely orange 98



Couplet 97

98(97)A. First tergum with a single rounded longitudinal bulge .... ***A. brianharrisi* n. sp.**

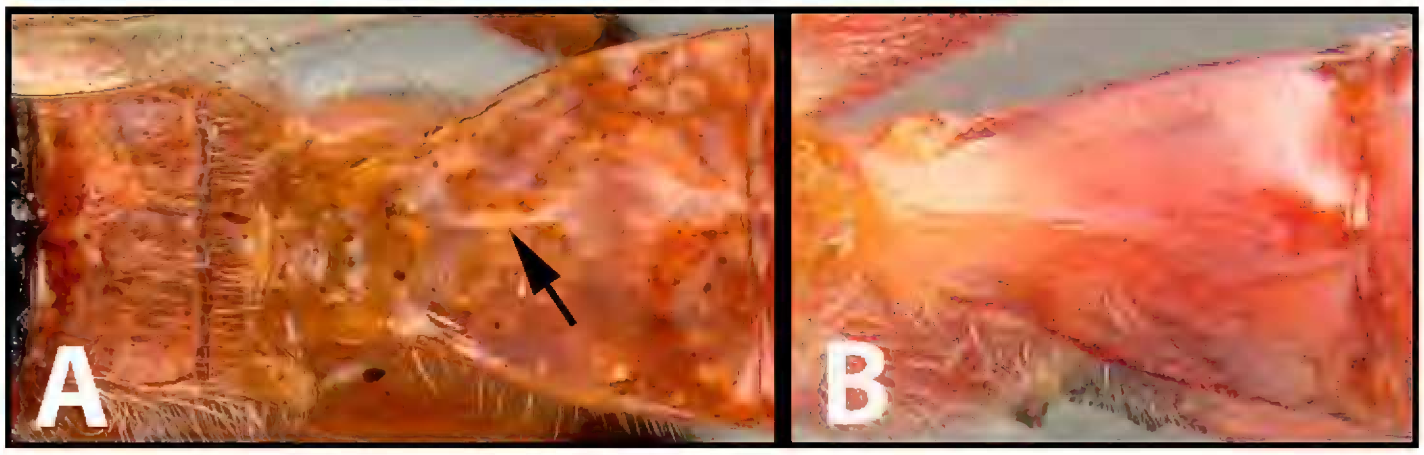
98(97)B. First tergum with two converging longitudinal carinae .... ***A. kaciejoae* n. sp.** male



Couplet 98

99(96)A. First tergum varying from weakly convex to with a rounded longitudinal bulge 100

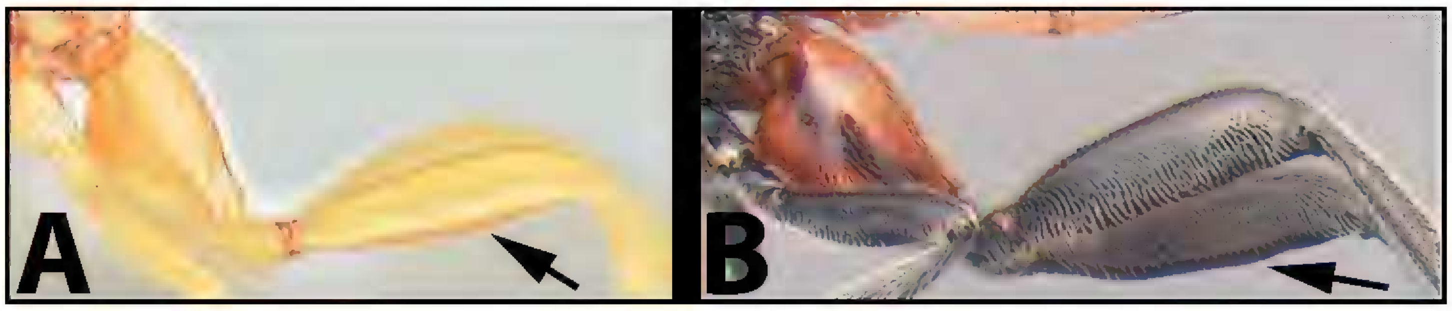
99(96)B. First tergum with well-defined median longitudinal carina 104



Couplet 99

100(99)A. Hind femur mostly or entirely pale 101

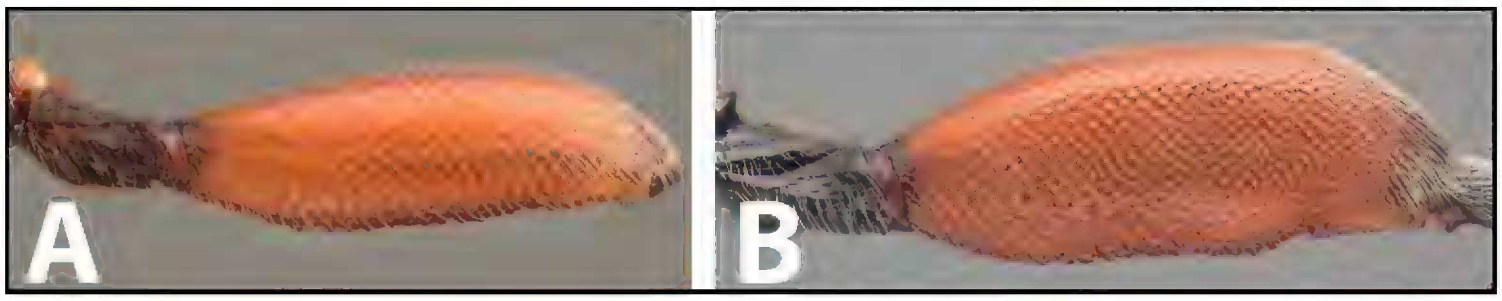
100(99)B. Hind femur mostly or entirely melanic 103



Couplet 100

101(100)A. Hind femur narrower 102

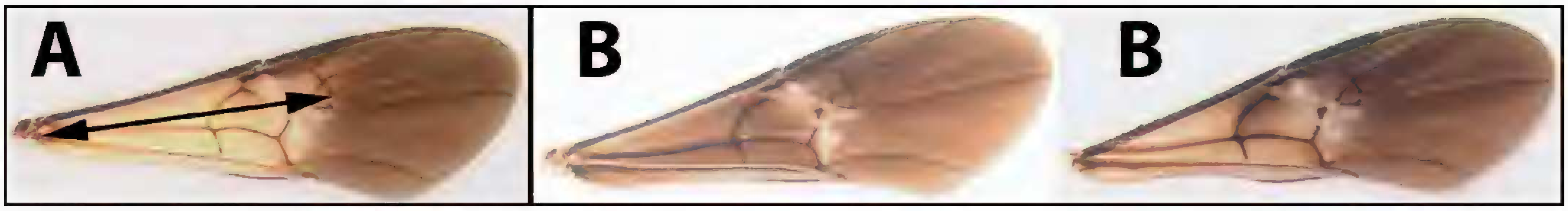
101(100)B. Hind femur wider .... *A. nicoya*



Couplet 101

102(101)A. Forewing with yellowish or clear area extending to the second submarginal cell .... *A. roibasi*

102(101)B. Forewing entirely infuscate or, if with yellowish or clear area basally, it does not extend to second submarginal cell (we cannot distinguish the following three species morphologically) .... ***A. jennyphillipsae* n. sp., *A. isidrochaconi* n. sp., *A. jeanfrancoislandryi* n. sp.**

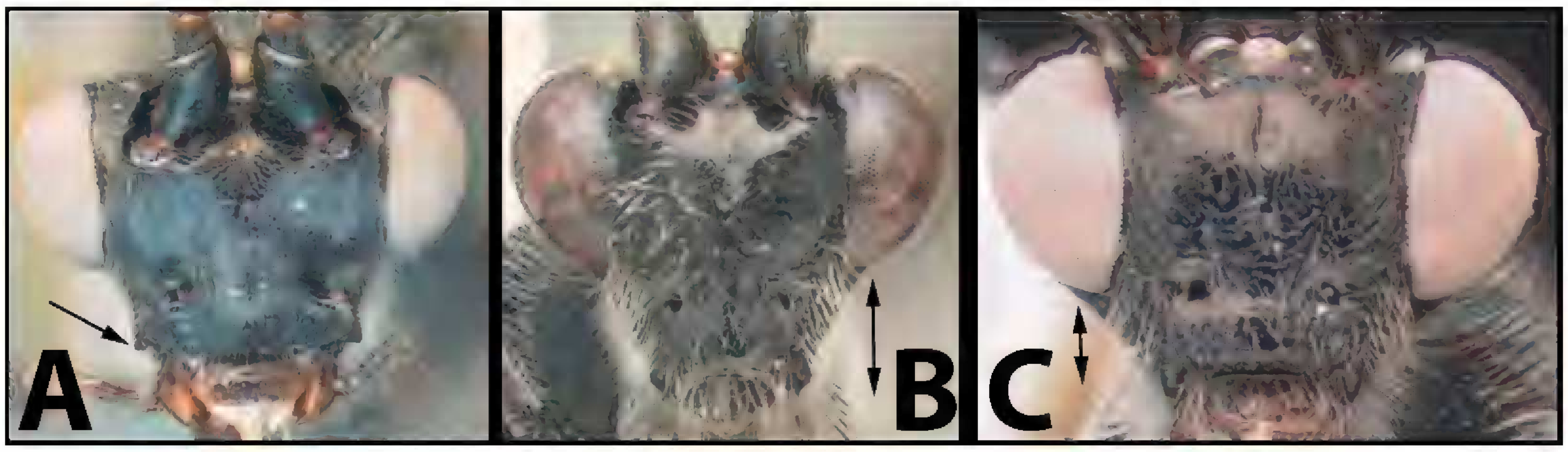


Couplet 102

103(100)A. Protuberance present lateral to clypeus; gena not elongate .... ***A. victoriapookae* n. sp.**

103(100)B. Protuberance absent lateral to clypeus; gena elongate .... *A. arua*

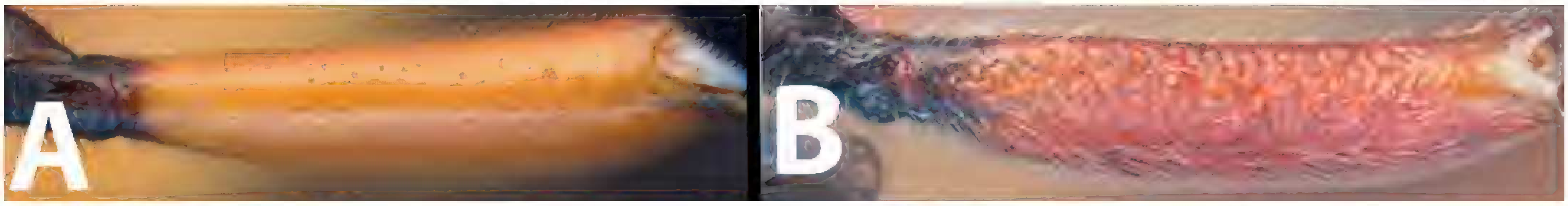
103(100)C. Protuberance absent lateral to clypeus; gena not elongate (the common state for *Alabagrus* species) .... ***A. jeanfrancoislandryi* n. sp.** males



Couplet 103

104(99)A. Hind femur with weak sparse punctures ventrally, little or no more heavily sculptured than dorsal surface .... ***A. sarahmeierottoae* n. sp.** male

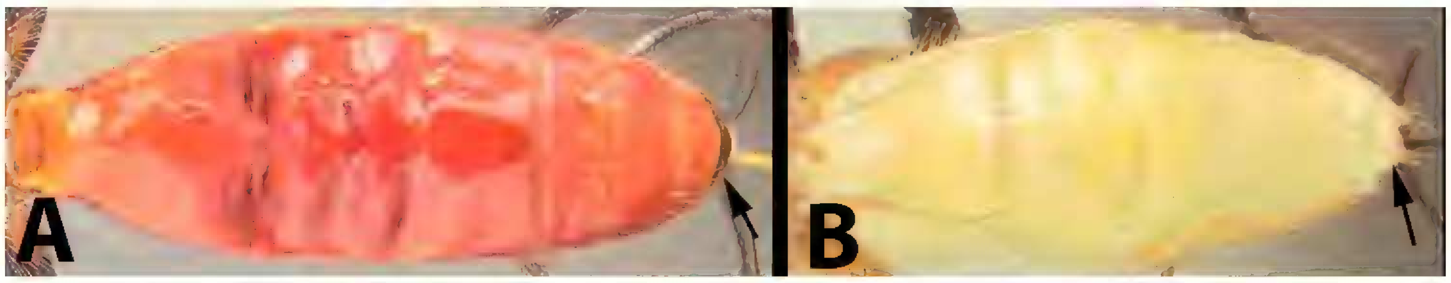
104(99)B. Hind femur heavily sculptured ventrally with aciculations or rugosities, distinctly more heavily sculptured than dorsal surface .... ***A. paulthiaucourti* n. sp.**



Couplet 104

105(82)A. Penultimate metasomal tergum (or more) melanic 106

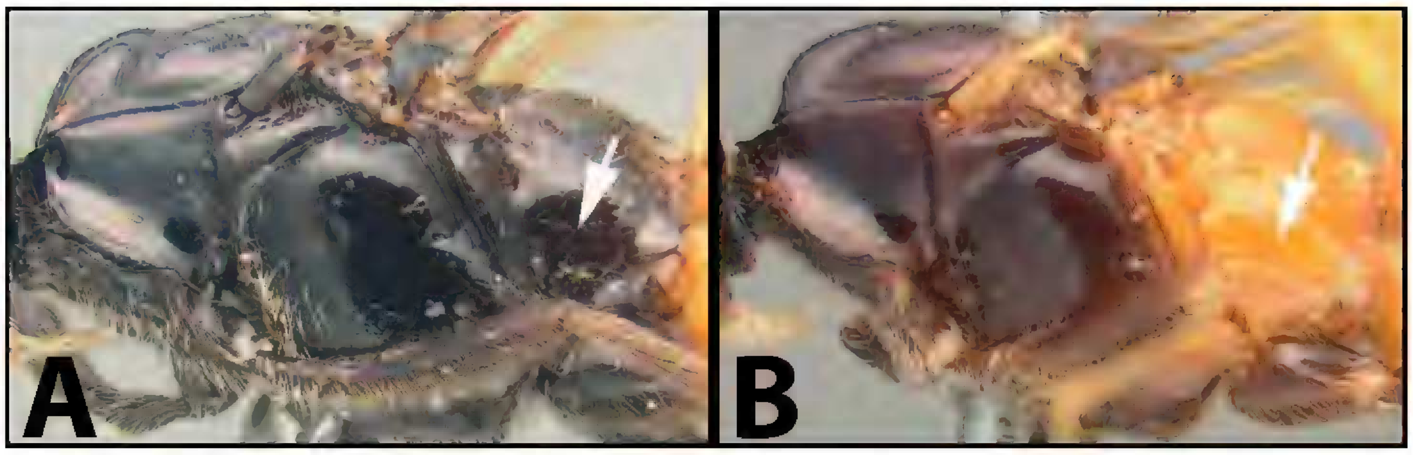
105(82)B. Penultimate metasomal tergum pale, reddish orange to yellow 107



Couplet 105

106(105)A. Metapleuron mostly or entirely melanic; propodeum melanic .... ***A. stiremani* n. sp.**

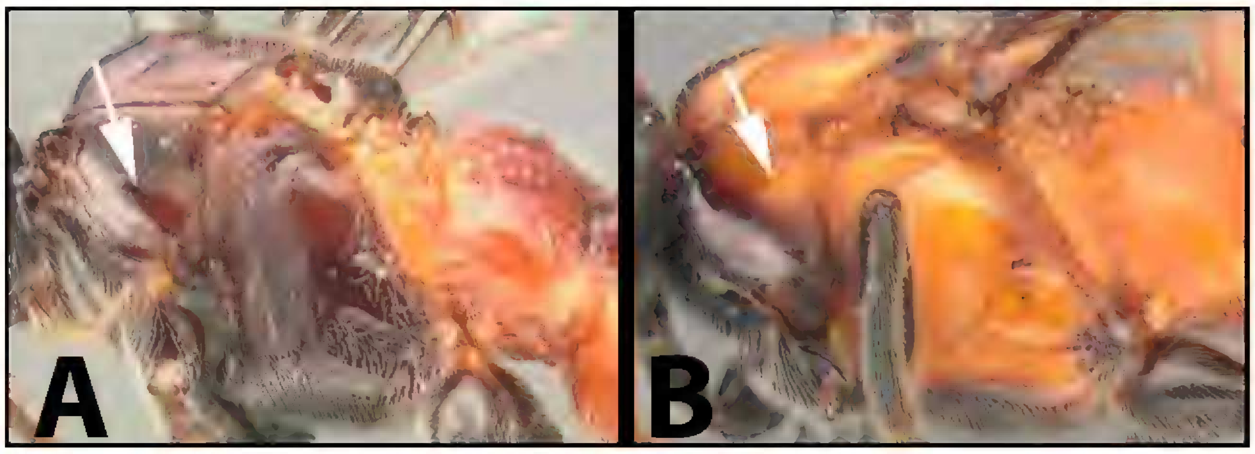
106(105)B. Metapleuron mostly or entirely pale; propodeum pale .... ***A. quickei* n. sp.**



Couplet 106

107(104)A. Pronotum entirely melanic 108

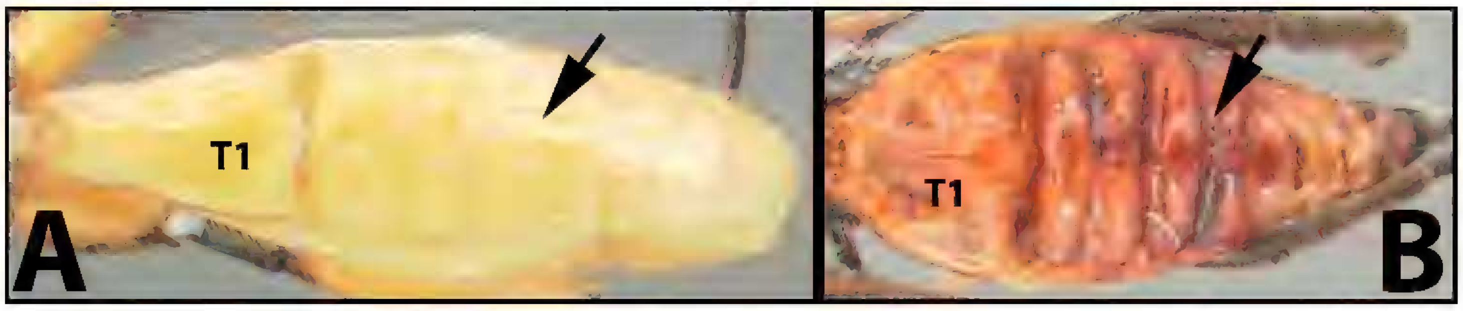
107(104)B. Pronotum partly or completely pale .... ***A. sarahsharkeyae* n. sp.**



Couplet 107

108(107)A. Third tergum lacking transverse depression or depression barely indicated; first tergum varying from weakly convex to with a rounded longitudinal bulge 109

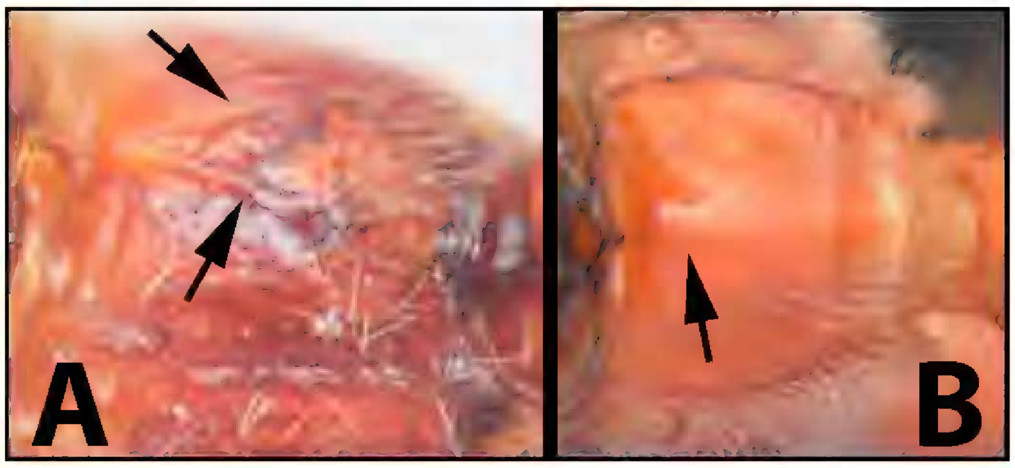
108(107)B. Third tergum with deep transverse depression; first tergum with well-defined median longitudinal carina .... *A. miqa*



Couplet 108

109(108)A. Propodeum sculptured, minimally with two diverging carinae anteriorly .... ***A. sarahmeierottoae* n. sp.** female

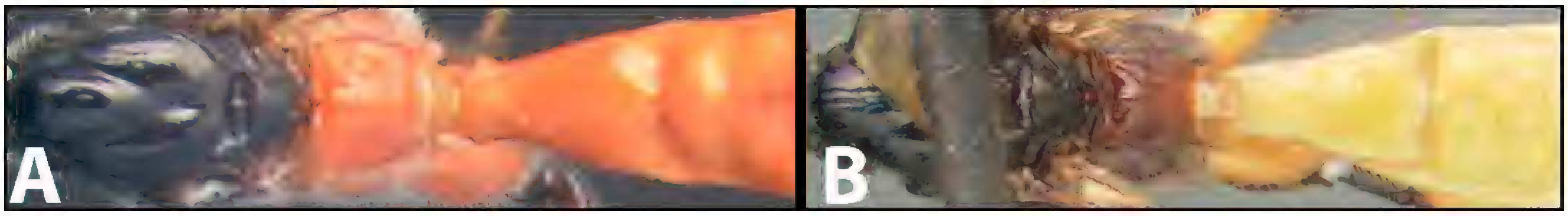
109(108)B. Propodeum completely smooth or with a slight bulge anteromedially 110



Couplet 109

110(109)A. Body melanic and orange .... *A. englishi*

110(109)B. Body melanic and yellow .... ***A. johnburnsi* n. sp.**

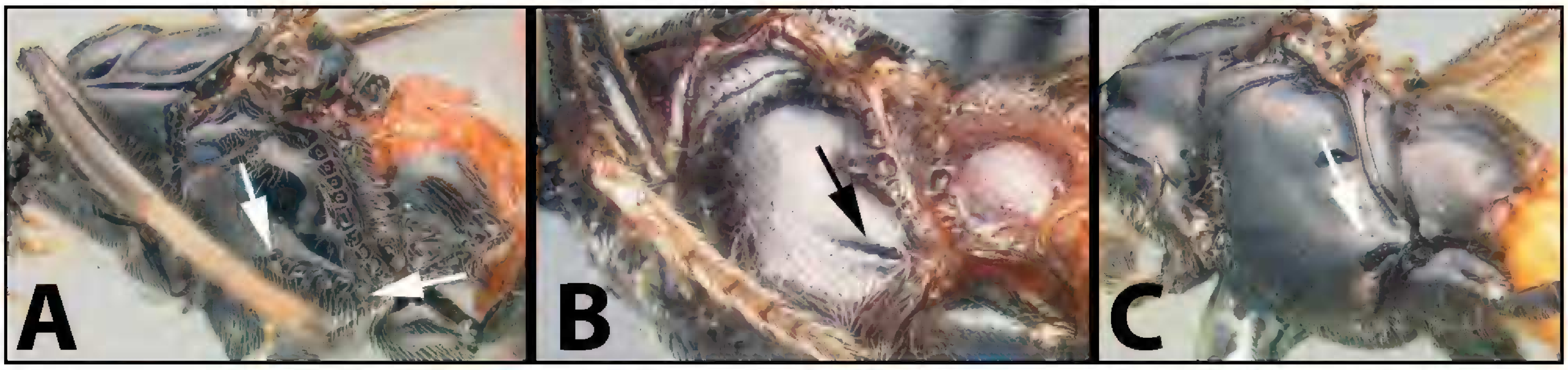


Couplet 110

111(78)A. Precoxal sulcus distinct and foveolate ½ or more length of mesopleuron 125

111(78)B. Precoxal sulcus with one or several distinct foveae posteroventrally with or without a smooth groove extending anteriorly, fovea not extending ½ length of mesopleuron 112

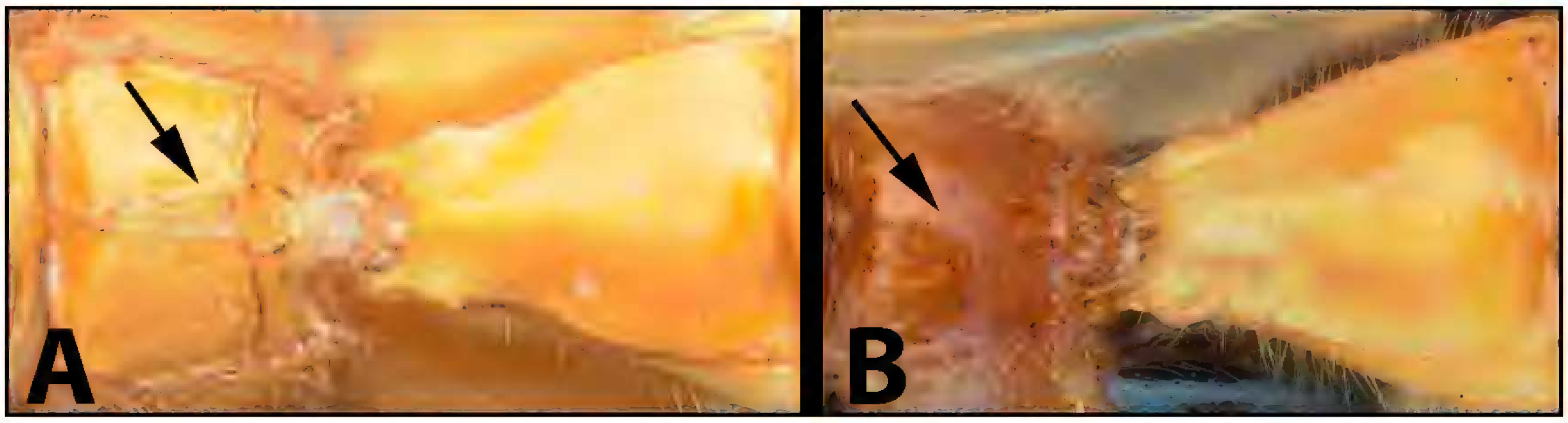
111(78)C. Precoxal sulcus absent or mostly absent, represented at most by small, shallow depression, usually posteriorly, crenulae always lacking 133



Couplet 111

112(110)A. Propodeum areolate, with at least one closed areola 113

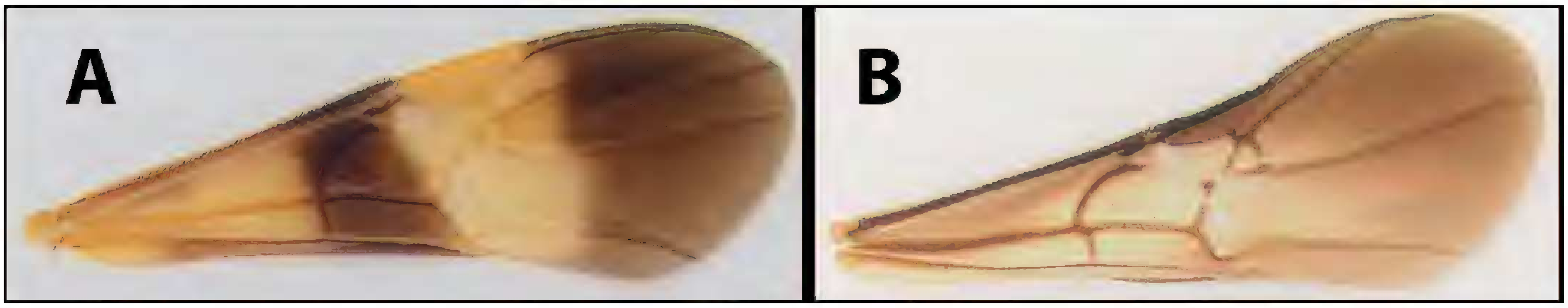
112(110)B. Propodeum lacking complete areolae, mostly smooth 117



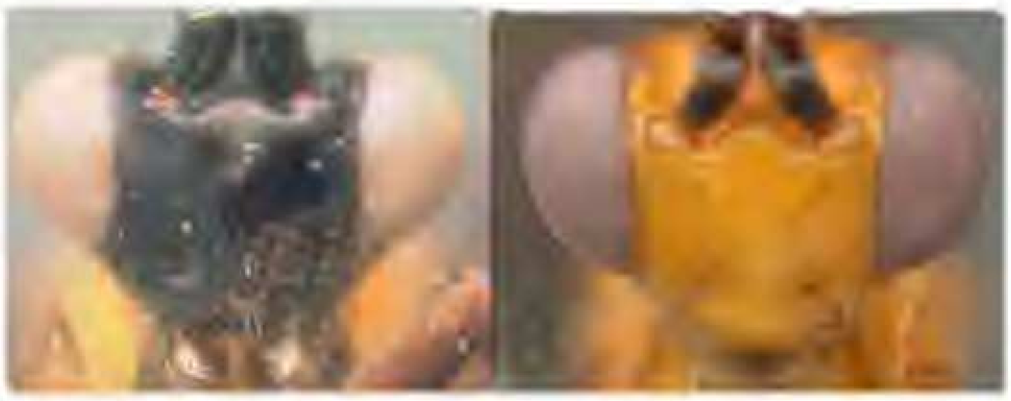
Couplet 112

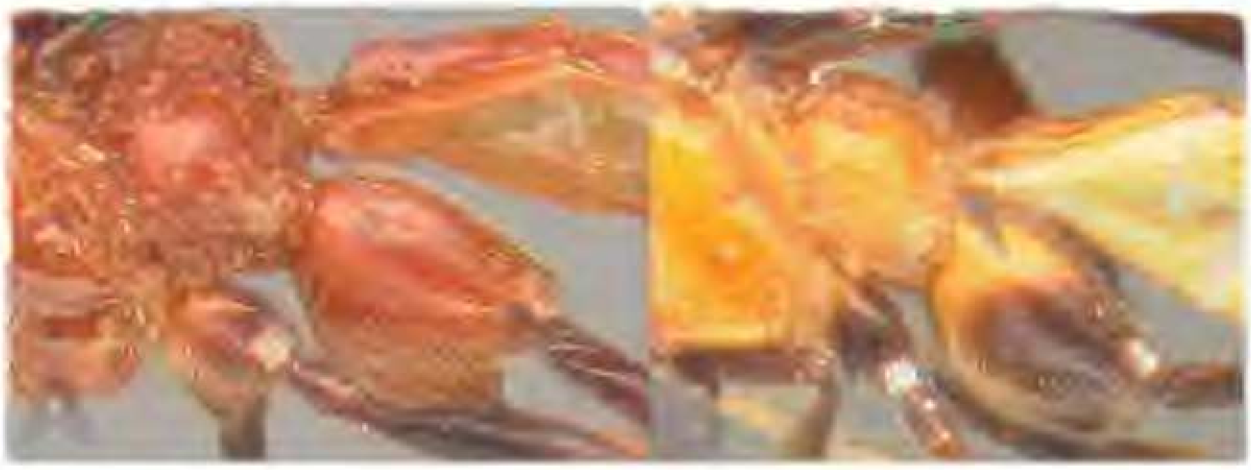
113(112)A. Forewing with 2 distinct yellow bands .... *A. voto*

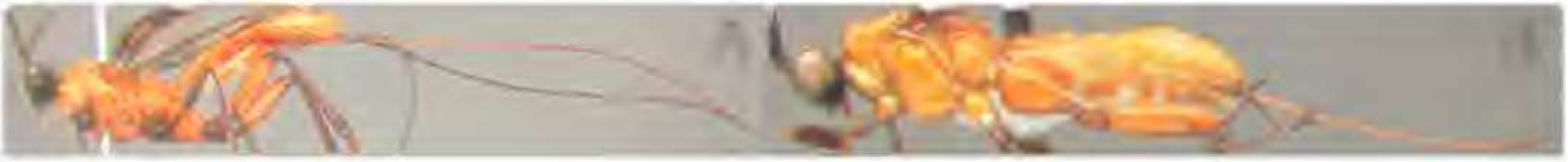
113(112)B. Forewing lacking 2 distinct yellow bands 114

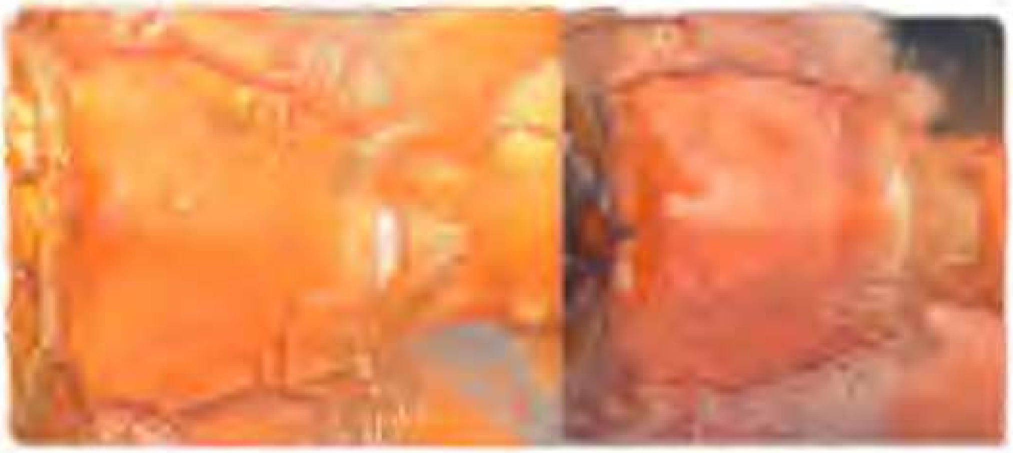


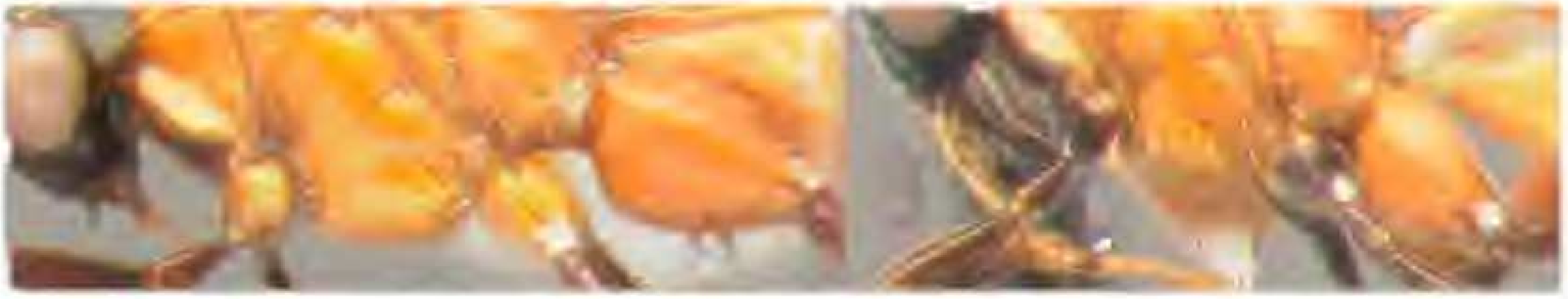
Couplet 113

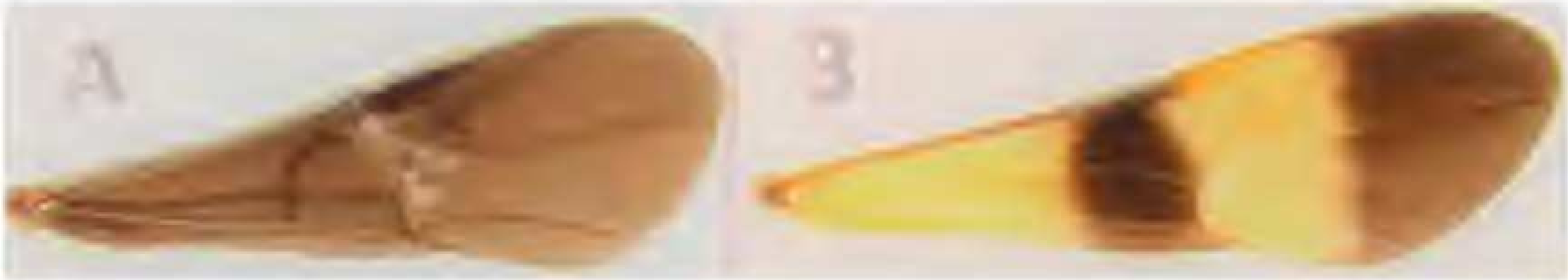











A
B